Available online at www.sciencedirect.com

ScienceDirect

Physics of Life Reviews 32 (2020) 1–40

PHYSICS of LIFE reviews

www.elsevier.com/locate/plrev

Review

Long transients in ecology: Theory and applications

Andrew Morozov [a,j], Karen Abbott [b], Kim Cuddington [c], Tessa Francis [d], Gabriel Gellner [e], Alan Hastings [f,k], Ying-Cheng Lai [g], Sergei Petrovskii [a,l,*], Katherine Scranton [h], Mary Lou Zeeman [i]

[a] *Mathematics, University of Leicester, UK*
[b] *Biology, Case Western Reserve University, USA*
[c] *Biology, University of Waterloo, Canada*
[d] *Tacoma Puget Sound Institute, University of Washington, USA*
[e] *Integrative Biology, University of Guelph, Canada*
[f] *Environmental Science and Policy, University of California, Davis, USA*
[g] *Electrical, Computer and Energy Engineering, Arizona State University, Tempe, USA*
[h] *Ecology and Evolutionary Biology, Yale University, USA*
[i] *Mathematics, Bowdoin College, Brunswick, USA*
[j] *Shirshov Institute of Oceanology, Moscow, Russia*
[k] *Santa Fe Institute, Santa Fe, New Mexico, USA*
[l] *Peoples Friendship University of Russia (RUDN University), Moscow, Russia*

Received 6 September 2019; accepted 9 September 2019
Available online 13 September 2019
Communicated by J. Fontanari

Abstract

This paper discusses the recent progress in understanding the properties of transient dynamics in complex ecological systems. Predicting long-term trends as well as sudden changes and regime shifts in ecosystems dynamics is a major issue for ecology as such changes often result in population collapse and extinctions. Analysis of population dynamics has traditionally been focused on their long-term, asymptotic behavior whilst largely disregarding the effect of transients. However, there is a growing understanding that in ecosystems the asymptotic behavior is rarely seen. A big new challenge for theoretical and empirical ecology is to understand the implications of long transients. It is believed that the identification of the corresponding mechanisms along with the knowledge of scaling laws of the transient's lifetime should substantially improve the quality of long-term forecasting and crisis anticipation. Although transient dynamics have received considerable attention in physical literature, research into ecological transients is in its infancy and systematic studies are lacking. This text aims to partially bridge this gap and facilitate further progress in quantitative analysis of long transients in ecology. By revisiting and critically examining a broad variety of mathematical models used in ecological applications as well as empirical facts, we reveal several main mechanisms leading to the emergence of long transients and hence lays the basis for a unifying theory.

Keywords: Transient dynamics; Ghost attractor; Transient chaos; Slow-fast systems; Regime shift; Pattern formation

---

[*] Corresponding author.
E-mail address: sp237@leicester.ac.uk (S. Petrovskii).

https://doi.org/10.1016/j.plrev.2019.09.004

1. Introduction

Obtaining reliable long-term predictions is a major issue in ecology, epidemiology and climate science, and it is a big challenge for sustainable ecosystem management [1]. Reliable forecasting is difficult due to the complexity of dynamics of underlying biological systems. Predictions can be sensitive to initial conditions and small perturbations, especially if the system's dynamics exhibit chaos [2–4]. Exogenous and endogenous noise that is ubiquitous in natural systems can substantially reduce predictability in a number of ways [5–7]. Additionally, insufficient information about feedbacks and species trophic responses can make prediction unreliable due to the structural sensitivity [8–10].

Reliable forecasting is further complicated by the phenomenon known as the 'regime shift': a sudden qualitative change in the ecosystem's dynamics [11–14]. Should such a change happen, any conclusions or estimates based on the observations made before the regime shift become irrelevant after the shift. However, the timing of the regime shift is difficult to predict and the problem of identifying early warning signals remains largely open. Regime shift often results in a population collapse and extinction of species, making it an important issue for nature conservation and ecosystem management. Previously regime shifts have been linked to a slow change in ecological parameters [11–14] which, under certain conditions, can push the system over the 'tipping point' (bifurcation) resulting in dramatic changes in the ecosystem properties (e.g. disappearance of a positive steady state). In its turn, variation of parameter values can appear as a consequence of an exogenous process such as, for instance, global climate change.

More recently, it has been shown that regime shift can be a property of long transient dynamics [15] – an alternative explanation that does not require a parameter change. Traditionally, long-term dynamics have been thought to correspond to the asymptotic behavior of the biological system, where trajectories have settled on some 'final state' (e.g. an equilibrium or a cycle). However, there is a growing body of empirical evidence and modeling studies showing that transient behavior and especially long transients play a pivotal role in the dynamics of ecosystems [16–21]. A similar paradigm shift is happening in epidemiology as well as other life sciences such as neuroscience and embryonic development [22–24], in climate modeling and other natural sciences [25–27]. The necessity of shifting the main focus from model attractors to transient dynamics lies in the very nature of biological systems: they often experience perturbations (external and/or internal) that can prevent them not only from reaching an attractor in the large-time limit but even from coming close to it [28]. Approximating the system's dynamics by considering it in the vicinity of an attractor then becomes irrelevant. Moreover, the time horizons of prediction in ecological practice and of action in ecosystem management are often considerably shorter than the relaxation time of the corresponding biological system [21].

The presence of long transients may provide an alternative explanation of sudden regimes shifts which may lead to species extinction and biodiversity loss. Indeed, the original mechanism of the regime shift mentioned above ('tipping point') that relates it to a change in ecological parameters is not universal, as sudden changes in ecosystem properties are not necessarily preceded by a noticeable change in the environment [29,30,15]. An ecosystem exhibiting long transient dynamics would typically show a similar behavior to that observed in a tipping point-type regime shift: an apparently stable dynamical regime suddenly experiences a fast transition to another regime or state (e.g. extinction). However, the appropriate ecosystem management response would be quite different in the case of tipping points and long transients [21]; it is therefore important to distinguish between the two scenarios.

Long transients observed empirically in biological and ecological systems have been frequently reported in the literature; see [15] for a brief review. Long transient dynamics have also been seen in a number of mathematical and computational models across several disciplines, e.g. [25–27]. Surprisingly, a regular consideration of this highly relevant phenomenon in the context of life sciences is lacking. In spite of a large number of specific examples available, there is a lack of understanding with regard to the factors that may result in long transients, the types of the corresponding regime shifts, early warning signals, etc. Any consistent classification of transients according to the mechanisms causing them is largely missing. In particular, the important open question is what is the relation, if any, between long transients and the tipping point phenomena.

This study intends to partially bridge the above gaps by providing a more systematic approach to mathematical modeling of long transients in biological systems, with emphasis on ecological applications, combining theoretical arguments with empirical observation. In doing that, particular attention is paid to the scaling laws of the long transients, i.e. how the lifetime of long transients depends on the controlling parameters of the system.

It should be mentioned here that, although transients have been emphasized more and more in recent studies, the ecological background for this work in fact draws on a much longer legacy. Importance of transients is inherently linked to the broader area of the nonequilibrium concept of ecological systems. A full treatment of these ideas is far beyond the current paper, but a look at some classic papers both helps to show the development within ecology of transient thinking, and emphasizes the importance of the more structured approach that we take here. More recent examples are referred to in our recent review [15] and are used to illustrate the ideas that we develop in the current paper. Some of the earliest work focused on moving away from the single climax state as the end point of succession in plant communities [31] and this idea of cyclic succession was essentially one that suggested that many ecosystems were in a transient state. This line of thinking developed into ideas that multiple stable states are coupled with transitions between states, and there is good experimental evidence for that [32]. Thus, the states referred to as stable are definitely not stable in a mathematical sense and this essentially means that the underlying ecological systems are best thought of as in a transient state.

Ideas that suggested the importance of transients were not limited to plant succession. For freshwater lakes, the paradox of the plankton as presented by Hutchinson [33] essentially says that these systems are not at their asymptotic state. The role of disturbance and the intermediate disturbance hypothesis as emphasized for tropical systems, both terrestrial and marine, by Connell [34], could also be viewed as an expression of the idea that ecological systems are best viewed in transient states. The view that equilibrium is not the right way to think of ecological systems also formed the basis for influential books by Botkin [35] and Rhode [36].

The paper is organized as follows. We first discuss an instructive definition of long transients in both deterministic and stochastic systems (Section 2). In Section 3, we classify the scenarios of transients in low-dimensional deterministic systems, relating them to different mechanisms, and revisit some conceptual mathematical models of population dynamics exhibiting long transients. In Section 4, we consider transients in stochastic systems and emphasize the role of noise in promoting transient dynamics. The impact of system complexity on transient behavior is further addressed in Sections 5 and 6 that deal with spatial systems and systems with time-delay, respectively. We then revisit the methods of data analysis and modeling aiming to reveal transients from empirical observation with an ultimate goal of anticipating possible regime shifts (Section 7). Finally, in Section 8, we summarize our findings and also briefly discuss the role of transients in decision making in long-term ecosystem sustainable management.

2. Setting the scene: what is a long transient?

Systematic consideration of a phenomenon should start with a definition that would pick up the phenomenon's essential features. Given the high complexity of long transient dynamics across a variety of biological systems, its very general definition is bound to be too broad and hence not instructive. Indeed, in the strict mathematical sense, one should refer to all non-asymptotic regimes (unless the model trajectory starts exactly on an attractor) as transients, which is not illuminating. However, we recall that here we are especially interested in long transients in the specific context of regime shifts.

Let us consider a certain dynamical regime. In the case that this regime persists without changing its properties (quantified by the average population densities, the amplitude of oscillations, Lyapunov exponents etc.) indefinitely, then it corresponds to the asymptotical system's dynamics. For convenience, we refer to such a regime as stable dynamics. In the case that it persists for a finite but sufficiently long time, we call this dynamics quasi-stable. The first point to clarify is when the duration of the given regime can be regarded as 'long'. In the ecological context, it means that it is much longer than the generation time of the considered species (for a brief review of specific cases see [15]). In a somewhat more theoretical context, the duration is long if it is much longer than any characteristic time of the regime (e.g. the period of oscillations).

Definition. Consider a system where all parameters (such as population growth rate, mortality rate, etc.) are constant, i.e. do not depend on time. We call the system's dynamics a long transient if one of the following two properties hold:

(a) apparently stable system's dynamics (a 'quasi-stable regime' that goes on for a long time) at some point experiences a fast transition to another regime, stable or quasi-stable. This transition occurs on a timescale much shorter than the duration of the preceding dynamical pattern;
(b) the system's dynamics evolve with time 'very slowly' over a timescale much longer than any characteristic time of the current dynamical pattern (e.g. the period of oscillations). This evolution of the dynamics properties eventually brings the system to a stable or to a different quasi-stable regime.

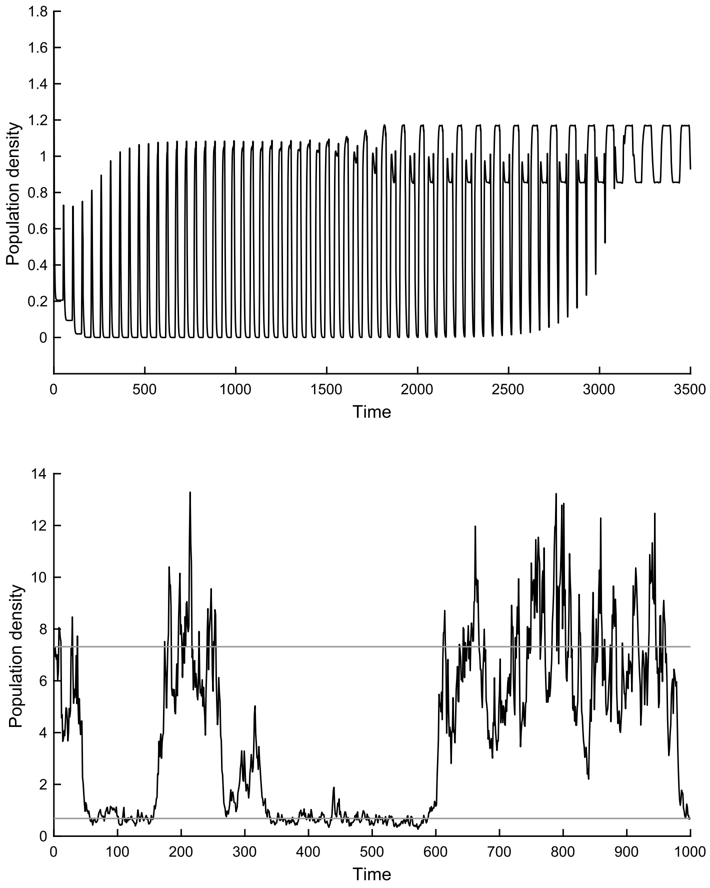


Fig. 1. Illustrative examples of the regime shifts in population dynamics models. (Top) Long transient dynamics in a model of structured population with time delay. Large-amplitude periodic oscillations of the population density that are persistent over dozens of generations suddenly evolves quickly to oscillations with a much smaller amplitude and a significantly different mean. From [37], adapted. (Bottom) Alternating steady states in a bistable single-species model with noise. The system spends a considerable time in a vicinity of one of the states (experiencing random oscillations around the average value shown by the horizontal line) before undergoing a fast transition to the other state. An observer who collects the information about the system's dynamics on a time scale much shorter than the system life-time in any one of the two transient states state can easily mistake it for an asymptotic state. From [40], adapted.

What is meant by 'long' in the above definition is, however, not clear until it is made more quantitative. An important benchmark of a long transient is the scaling property of its average lifetime. In either of the above cases, the average lifetime of the transient regime is described by a scaling function (e.g. exponential or the power law) of a controlling parameter, say p. There can be two possibilities: (i) there exists a finite critical value p_c such that the average lifetime tends to infinity when $p \to p_c$, or (ii) the average lifetime tends to infinity when p tends to infinity. In other words, 'long' in our definition means that the transient's lifetime can be made arbitrarily long by choosing the value of the controlling parameter appropriately. Parameter p can either have an immediate biological or physical meaning (growth or mortality rates, size of the spatial domain, noise intensity, etc.) or it can appear as a combination of the original parameters, e.g. being the largest eigenvalue of the system in a given steady state. More details will be given later, e.g. see Eqs. (5), (13), (19)–(20) and Tables 1 and 2.

The above definition is based on observed patterns of dynamics both in real-world systems and in relevant models of ecological dynamics. Note that scenario (a) resembles the regime shift due to the tipping point mechanism; however, in our case there is no tipping point as all the system's parameters are constant. We further observe that long transients can occur in both deterministic and stochastic systems (although due to different mechanisms). Two different examples of long transient behavior in population models are shown in Fig. 1. The top panel of Fig. 1 demonstrates a transition occurring in a fully deterministic system from the transient, quasi-stable regime of large-magnitude oscillations to the final, asymptotic regime of small-magnitude oscillations (a closer look reveals that the period of oscillations changes too [37]). The bottom panel shows the regime of alternative phases (intermittency) in a population model with noise. In this case, each consecutive phase can be regarded as a transient regime and the entire system's dynamics are a sequence of transients. Thus, the post-transitional regime can be either asymptotic or transient as well. In the latter case, the existence of long transients can be linked to the geometrical properties of the system's attractor. For instance, in the Lorenz model of deterministic chaos with one saddle and two unstable focuses [38,39], the irregular switches between one focus to the other may occur very fast but occasionally take a much longer time. Another example will be considered in detail in Section 3.1.

The existence of a scaling law for the long transient's lifetime (average lifetime in case of stochastic systems) is an important property of long transients. This is a property that makes possible their classification (as will be examined and explained throughout this paper). Also it creates a link between empirically observed long transients (e.g. counted in numbers of generations) and the general framework of dynamical systems, thus enabling the application of powerful methods of quantitative analysis. In particular, tools of the bifurcation theory in many cases allow us to refine the specific mechanisms behind long transient dynamics by identifying a few simple, "conceptual" (yet biologically meaningful) models that exhibit long term transients with different properties. This will be done in the next section.

3. Long transients in low-dimensional deterministic models

3.1. Saddle points and crawl-by dynamics

Our analysis is based on a presumption common in theoretical studies that an ecosystem can be regarded as a complex dynamical system whose properties arise as a result of interaction between many different factors and processes acting across a broad range of spatial and temporal scales. However, the high complexity of a real-world system does not necessarily require a similarly high complexity of its mathematical description. It often happens that some important general properties of the system can be grasped by a relatively simple model [2,4,41].

We start with a deterministic, nonspatial case; extension of our approach onto spatial systems will be discussed in Section 5. A system of n interacting species can be described mathematically in a variety of ways. The two most commonly used approaches are given by either a system of ODEs (ordinary differential equations):

$$\frac{du_k(t)}{dt} = f_k(\mathbf{u}), \quad k = 1, \ldots, n, \tag{1}$$

where $\mathbf{u} = (u_1, \ldots, u_n)$ and u_k is the population density of the kth species at continuous time t, or by a system of discrete-time maps:

$$u_k^{i+1} = F_k(\mathbf{u}^i), \quad k = 1, \ldots, n, \quad i = 1, 2, \ldots, \tag{2}$$

where $u_k^i = u_k(t_i)$ is the density of the kth species at the ith step in time and discrete time is usually measured in either generations or years. In our analysis below, we will consider (1) as a paradigmatic dynamical system; however, most of the results appear to be generically valid for discrete-time systems too.

The traditional way to reveal the properties of the ecosystem in terms of the corresponding dynamical system (1) is to consider its asymptotic properties, i.e. where the system's trajectories go in the large-time limit. The corresponding set in the phase space is called the ω-limit set. In particular, ω-limit sets include all attracting invariant sets of the system, such as, depending on the system's dimensionality, stable equilibria (steady states), stable limit cycles, tori and chaotic attractors.

Whilst the attracting invariant sets determine the properties of the system in the large-time limit, the system's behavior at small and intermediate times is to a large extent shaped by non-attracting invariant sets (NAIS) – in the cases where they exist. In particular, the presence of NAIS can lead to the emergence of long transients (an alternative mechanism not related to NAIS will be considered in Section 3.2). In the baseline case where the NAIS is an unstable steady state (unstable focus or node, or saddle), the emergence of long transients is readily seen. Let $\bar{\mathbf{u}} = (\bar{u}_1, \ldots, \bar{u}_n)$ be a steady state of system (1). Considering the system's dynamics in a small vicinity of $\bar{\mathbf{u}}$, Eqs. (1) can be linearized resulting in

$$\frac{dx_k(t)}{dt} = a_{k1}x_1 + \ldots a_{kn}x_n, \qquad k = 1, \ldots, n, \tag{3}$$

where $x_k(t) = u_k(t) - \bar{u}_k$ are the deviations from the steady state (assumed to be sufficiently small in order to make the linear approximation valid) and $a_{ij} = \left(\partial F_i/\partial u_j\right)_{\mathbf{u}=\bar{\mathbf{u}}}$. Considering for the sake of simplicity the case where all eigenvalues $\lambda_1, \ldots, \lambda_n$ of system (3) are different, its general solution is a linear combination of exponential functions $e^{\lambda_i t}$. Let λ_1 be the eigenvalue with the largest real part and $\mathrm{Re}\,\lambda_1 > 0$. Assuming that at a certain moment the system is close to the steady state (e.g. because of the corresponding initial conditions), the rate at which the system moves away[1] is then determined by the term $e^{(\mathrm{Re}\lambda_1)t}$ and hence by the exponent $\mathrm{Re}\lambda_1$. Correspondingly, the time scale τ at which the system remains in the vicinity of the unstable steady state is inversely proportional to the exponent:

$$\tau \propto \frac{1}{\mathrm{Re}\,\lambda_1}. \tag{4}$$

Obviously, in case $\mathrm{Re}\,\lambda_1$ is small the time that the system spends close to the unstable steady $\bar{\mathbf{u}}$ can be very long. Hence, the system exhibits a long-term transient behavior. Note that system (3) is linear. Therefore, although long transients play a more prominent role in nonlinear systems (as will be explained below), they can occur already in a linear system.

Defining the controlling parameter as $p = \mathrm{Re}\lambda_1$, the lifetime of the transient scales with p as a power law:

$$\tau \propto p^{-1}. \tag{5}$$

The unbounded growth in τ when the parameter approaches its critical value $p_c = 0$ is a generic property of the system behavior in the vicinity of the equilibrium. This agrees with our definition of long transients in Section 2. Note that the power-law type scaling relation (5) is conventional rather than absolute as it can change to a function of a different kind if the controlling parameter is chosen differently. For instance, if the system is predominantly considered in the parameter range close to the bifurcation, i.e. where $\mathrm{Re}\lambda_1 \ll 1$, it may be more convenient to define the control parameter as $p' = -\ln(\mathrm{Re}\lambda_1)$. It is readily seen that relation (4) then turns into an exponential function instead of the algebraic:

$$\tau \propto e^{p'}, \tag{6}$$

with the transient lifetime tending to infinity for $p' \to \infty$.

Note that the above analysis is valid even when $\bar{\mathbf{u}}$ is an unstable focus or node, i.e. where all eigenvalues have positive real parts. However, in this case the long transients can only occur if the initial conditions are chosen already in a small vicinity of $\bar{\mathbf{u}}$. Although this is not entirely unrealistic, in the context of real-world dynamics it apparently requires some rather special conditions (an initial kick that would push the system close to the unstable state or a sudden change in the stability of the steady states) and hence may be regarded as a rare event. However, in case $\bar{\mathbf{u}}$ is a saddle, the range of relevant initial conditions is much broader because of the existence of the stable manifold (where in a general case the manifold can be multidimensional). Indeed, any point in the phase space that is initially close to the stable manifold, e.g. see area B in Fig. 2a, will be eventually brought by the system flow into the required small vicinity of the saddle and will stay there over the time given by estimate (4). The initial fast evolution of the system along the stable manifold is followed by the long transient quasi-stationary dynamics, also known as a "crawl-by" [15].

The effect of the initial conditions on the emergence of the crawl-by can become much less restrictive in a nonlinear system. In particular, in a two species system, this happens if there is a separatrix passing close to the saddle (see Fig. 2b), e.g. a limit cycle. In this case, trajectories starting in vast areas of the phase plane are channeled into the small vicinity of the saddle, hence leading to the emergence of the long quasi-steady state transient dynamics described by (4).

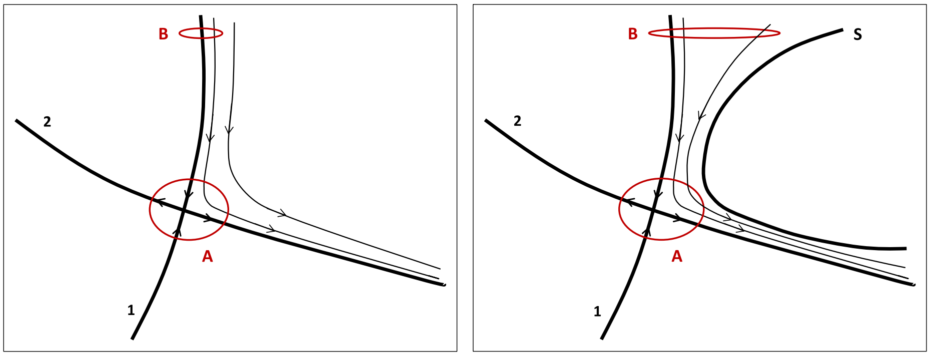
An example of an ecologically meaningful system exhibiting long transients due to the existence of a saddle point is given by the Rosenzweig–MacArthur prey-predator model [42] which is characterized by logistic growth of the prey and a Holling type II predator functional response:

$$\frac{du(t)}{dt} = \alpha u\left(1 - \frac{u}{K}\right) - \frac{\gamma u v}{u+h}, \tag{7}$$

$$\frac{dv(t)}{dt} = \frac{\nu\gamma u v}{u+h} - m v, \tag{8}$$

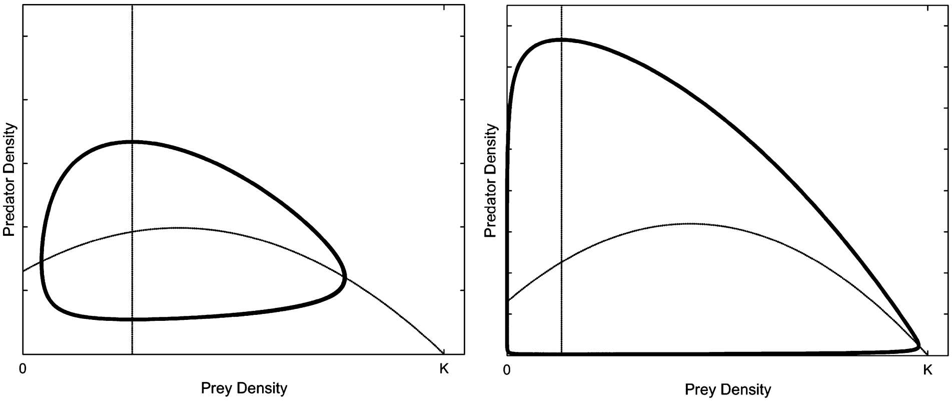
---

[1] Here and below, by saying "system moves" or "system goes" we mean the corresponding solution.



(a) (b)

Fig. 2. A sketch of phase plane with a saddle point. Attracting and repulsing manifolds of the saddle are shown by curves 1 and 2, respectively. (a) In order to get into the small vicinity (red circle A) of the saddle point where the system can spend a considerable time creating a long transient, see Eq. (4), the initial state must lie close to the attracting manifold (domain encircled by red curve B). (b) Same as in (a) but now there is a separatrix S lying close to the saddle. The trajectories starting in a broad area of the phase plane (e.g. the domain encompassed by red curve B) are channeled to the small vicinity of the saddle.

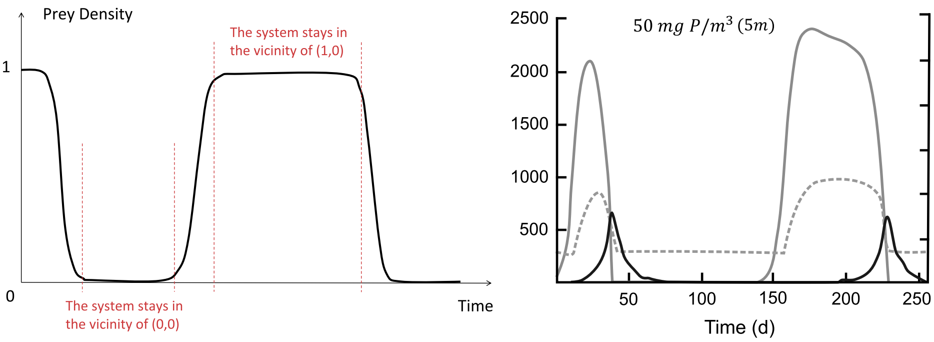


(a) (b)

Fig. 3. Phase plane of the prey-predator system (7)–(8). The intersection of the two isoclines (shown by the thin lines) produces the coexistence steady state. For a sufficiently large carrying capacity K, the steady state is unstable and is surrounded by a stable limit cycle (shown by the thick line). (a) For K just beyond the Hopf bifurcation, the size of the cycle is small. (b) With an increase in K the cycle grows in size and closely approaches the two saddle-points $(0, 0)$ and $(K, 0)$.

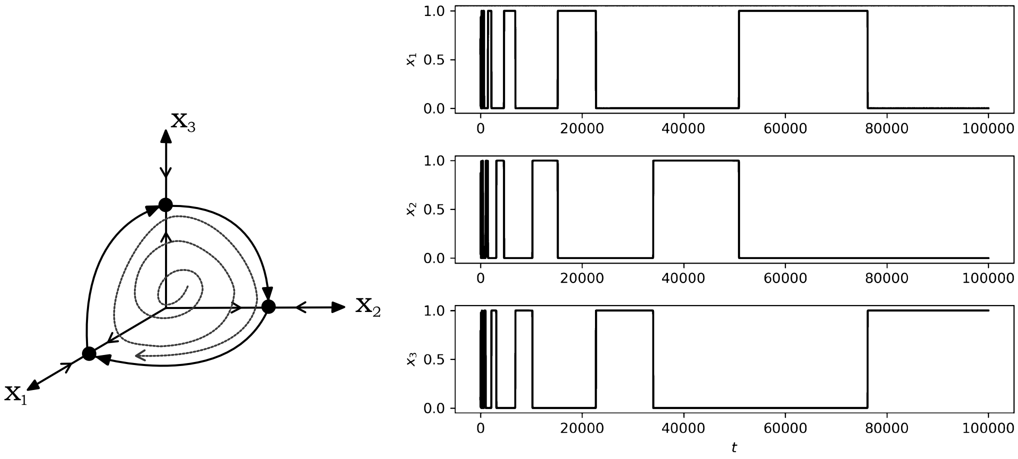
where u and v are the densities of prey and predator, respectively, and the parameters have their usual meaning [42, 43]. It is readily seen that, depending on parameter values, this system can have up to three steady states, i.e. boundary steady states $(0, 0)$, $(K, 0)$ and the positive (coexistence) steady $(\bar{u}, \bar{v})$. In a broad range of parameter values, system (7)–(8) is known to exhibit an oscillatory behavior, which corresponds to a stable limit cycle in its phase space (see Fig. 3) emerging in a Hopf bifurcation when the coexistence state loses its stability. With parameters moving further away from the Hopf bifurcation point (in this case, the boundary steady states are saddles), the limit cycle grows in size and eventually approaches very close to the saddle-points $(0, 0)$ and $(K, 0)$ (see Fig. 3b). This is exactly the kind of situation shown in Fig. 2b. The closer the system approaches a saddle point, the slower it moves along its trajectory in the phase plane, and hence the longer it stays in a close vicinity of each of the unstable steady states (Fig. 4a): the long term transient behavior emerges. We mention here that dynamics with similar properties are observed in more realistic and more complicated models [29,44] (see Fig. 4b) which points out at the generality of the suggested mechanism.

Note that, contrary to the baseline case shown in Fig. 2, in the above example of the Rosenzweig–MacArthur model the dynamical system possesses not a single saddle-point but two saddles forming a heteroclinic connection. Correspondingly, there are two transient quasi-stationary states. Due to the existence of the stable limit cycle passing



(a) (b)

Fig. 4. (a) Population density vs time as predicted by a prey-predator system with two patterns of crawling-by behavior; in the corresponding parameter range the system becomes arrested when its trajectory in the phase plane comes too close to the two saddles (cf. Fig. 3b). (b) The biomass of *Daphnia* (black curve) and algae (grey curve) obtained in a realistic phytoplankton-grazer model [44] (the dashed curve shows algal C:P ratio). The system shows a long term transient behavior when it is arrested by the saddle-point at $(0, 0)$.



(a) (b)

Fig. 5. Long transients in the three species cyclic competition model. (a) The structure of the phase space of the model, the three boundary ‘one species only’ states are connected into a hereroclinic cycle. (b) The corresponding temporal dynamics showing transient quasi-stationary states of ever increasing duration.

through a close vicinity of these saddles, each of the two crawl-bys becomes recurrent. The entire system’s dynamics are a sequence of transients; long intervals of apparently stable quasi-stationary dynamics are connected by fast transitions between them (cf. Fig. 4a). For each of the crawl-bys, its lifetime is determined by the closeness of the limit cycle to the corresponding saddle showing an unbounded increase when the vertical isocline of the system approaches axis v.

Depending on the type of interspecific interactions and the number of species explicitly included in the model, the phase space of the system can be more complicated, e.g. contain several saddles. In the case where heteroclinic connections form a loop – a heteroclinic cycle – the overall asymptotic dynamics may become transient, i.e. the life time of the crawl-bys increases unboundedly in the course of time. One classical example of such behavior is a system of three cyclically competing species (known as well as the rock-paper-scissors game) [45,46]. In this system, there are three boundary steady states where only one species is present and the other two are absent; these three states are connected together into an attracting heteroclinic cycle (see Fig. 5a). The system’s trajectory eventually approaches the cycle infinitesimally close, correspondingly passing closely to each of the boundary states in turn, hence creating the transient quasi-steady states where the density of one species is approximately at its carrying capacity and the densities of the other two species are very small (Fig. 5b). Since each new turn of the trajectory brings it closer and closer to

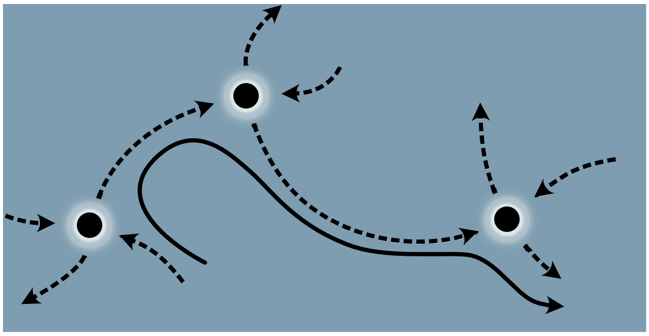


Fig. 6. A sketch of the phase space of a higher-dimensional (multi-component) system. Several saddles are linked by heteroclinic connections (dashed lines). A hypothetical system's trajectory (thick curve) lies close to the heteroclinic connections and hence passes close to the saddles, thus staying for a long time near one saddle before moving on to the next. From [53], adapted.

the boundary states, the time spent in the vicinity of the states is ever increasing with time. The transient's lifetime is scaled as $\tau \propto \pi^T$ where the quantity $\pi > 1$ depends on the species' growth rates and the competition coefficients, and $T = 1, 2, \ldots$ counts the number of cycles repeated over the entire loop [46]. We mention here that a similar transient behavior is shown by the Guckenheimer–Holmes cyclic model [47] and by a number of other models where transients include periodic or even chaotic solutions [48]. Although heterogenic cycles are not often seen in a general dynamical system, they are a common feature of dynamical systems with a symmetry [49]. Note that, generally speaking, the unbounded growth of the crawl-by's lifetime is not robust to noise. When noise is included into the model, its effect can stabilize the dynamics resulting in a finite lifetime of the transients.

Crawl-by behavior in real-world population dynamics has been observed in several field and laboratory studies. Evidence of long term transient behavior induced by saddle-points includes zooplankton-phytoplankton interaction in lakes [44] and various examples of cyclic succession of competing species such as side-blotched lizards [50] or competing bacteria [51] as well as some yeast strains [52]. In each case, a long term dominance of one species occurred before displacement by another species, in the full agreement with the prediction of the theory (cf. Fig. 5). A well-known example of crawl-by behavior in laboratory settings is the dynamics of the flour beetle *Tribolium* [29]. In the course of time, population dynamics of the beetle typically showed an onset of oscillations. However, in many cases the oscillatory dynamics were preceded by a long period of an approximately constant population size. An apparent explanation for the emergence of the quasi-stationary state is that the initial state of the system placed it close to a saddle point. Indeed, the corresponding population dynamics model that describes *Tribolium* dynamics quite accurately does possess a saddle in its phase space [29].

In a more complex, higher dimensional system (e.g. with a larger number of species), the transient dynamics can have more complicated properties. One possibility is given by a straightforward generalization of the above ideas. Consider a system where the phase space contains multiple saddle-points linked by heteroclinic connections (see Fig. 6). Apparently, this structure of the phase space may lead to the emergence of multiple quasi-steady states and multiple different crawl-bys respectively. A trajectory that at some moment comes close to the heteroclinic connection (e.g. by the choice of the initial conditions) will follow it closely, thus passing through a small vicinity of the saddles. The system then may stay in the vicinity of a saddle for a long time before following the heteroclinic connection to the next saddle [53]. Transition to a next saddle is likely to mean a significant change in the state variables: a regime shift occurs. (Note that from the point of an 'external' observer who is not aware about the phase space design such regime shift would happen without any obvious reason as the system's parameters remain constant.) After a number of such regime shifts due to the crawl-by behavior, the trajectory would either settle on an attractor in another part of the phase space or, if there is a stable limit cycle passing close to the saddles, will repeat its journey. Whilst in the former case each quasi-steady-state long transient will only happen once, in the latter case the long transients are recurrent. We mention here that, apart from the application of this mechanism to population dynamics [50,54] and to epidemiology [55], there have also been several studies where models with the above properties (existence of multiple connected saddles) were used to simulate neural activity behind the sense of smell [56,53] being motivated by experimental data obtained for zebrafish, locusts and other insects.

Note a long transient behavior of one system can be the asymptotic dynamics of another, modified system. As an example, consider the following generic dynamic system:

$$\frac{du}{dt} = f(u), \tag{9}$$

which has a stable equilibrium $\hat{u}$. Clearly, $\hat{u}$ is an asymptotic state for the system. If the system is two dimensional, i.e. $u = (u_1, u_2)$, one can easily modify it by multiplying the right-hand side in (9) by a suitably defined function $g(u)$ to change the eigenvalues of the equilibrium from the case with two negative eigenvalues to the case where one is positive, but arbitrarily small. In the new system,

$$\frac{du}{dt} = f(u)g(u), \tag{10}$$

$\hat{u}$ is a saddle; thus, it exhibits as a long 'crawl-by' transient the asymptotic behavior of the previous system (9). From this observation it is clear that any transient that is a saddle (crawl-by) could equivalently be the asymptotic behavior of a different system.

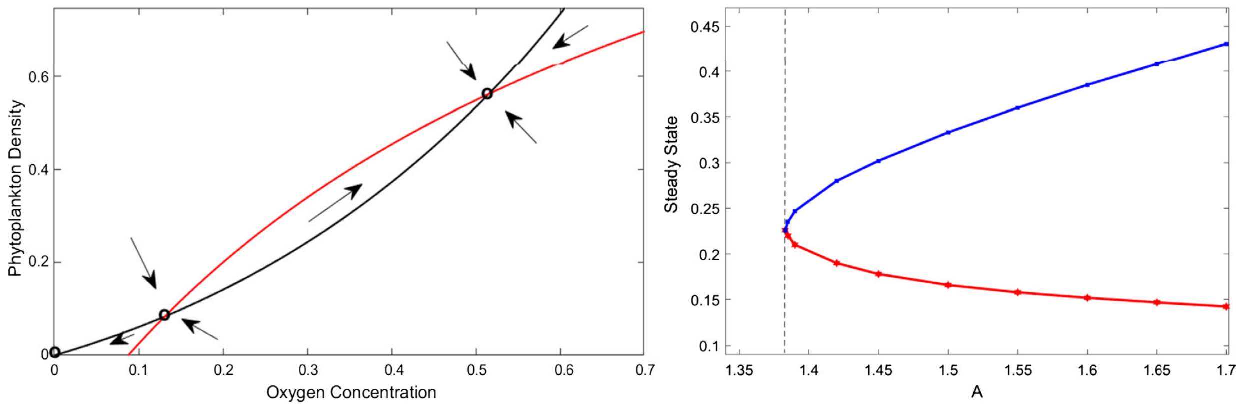
Apart from NAIS such as simple saddles and sets of connected saddles causing crawl-by behavior, a number of nonlinear models in ecology, epidemiology and economics demonstrate the existence of more complicated transient regimes known as chaotic saddles. Dynamical systems theory defines chaotic saddles as compact invariant sets which are neither attractors nor repellers and which contain a chaotic orbit with a positive dominant Lyapunov exponent [26,57]. For the transient chaos to emerge, there are restrictions on the system's dimensionality: the minimum dimension is two for invertible discrete maps and three for continuous flow systems. Chaotic saddles can arise in a crisis bifurcation (collision with another attractor), for instance, when a stable node collides with the basin of a chaotic attractor [58,27]. As a result of the crisis (collision), the chaotic attractor turns into a chaotic saddle: there emerges a channel (usually very narrow, ultimately of zero measure) through which the trajectory can leave the former chaotic attractor's basin to asymptotically approach another attractor. Correspondingly, the system's trajectories would normally stay close to the chaotic saddles for a long time before escaping it through the channel: a long term chaotic transient occurs. During this time, the dynamical system would exhibit behavior indistinguishable from that of the pre-bifurcation chaotic dynamics. The average lifetime of a chaotic transient typically scales with the bifurcation parameter as a power law. The existence of chaotic saddles was established both theoretically [59] and experimentally [60]. Also, a number of population models predict extinction of species via a long term transient chaos [61, 62].

Interestingly, although chaotic saddles possess the defining properties of a saddle (e.g. the existence of attracting and repulsing manifolds), they also can be considered from a different point of view taking into account their relation to a bifurcation changing the phase space properties. Namely, the emergence of chaotic saddles is often related to the so-called ghost attractors. This will be considered in details in the next section.

3.2. Ghost attractors

In the previous section we considered the long-term transient behavior occurring due to the system being close to the NAIS. A simple yet instructive example of this "crawl-by" dynamics is induced by a saddle-point in the phase space of the system. Once the system's trajectory brings it to the vicinity of the saddle, it can remain there for a considerable time; the closer to the saddle the system is and/or the smaller is the largest (positive) eigenvalue, the longer is the crawl-by's lifetime.

In this section, we consider an alternative mechanism where the observed system's dynamics have similar features, i.e. the system remains within a certain domain of the phase space for a considerable time mimicking an asymptotical behavior (e.g. steady-state, periodic or chaotic) yet not actually being asymptotics. The essential difference from the above is that now in that domain there is neither attractor nor NAIS. As we will show below, this can happen for parameter values close to a bifurcation that destroys the attractor. For parameters below their bifurcation value, there exists an attractor with the properties corresponding to those of the long transient; for parameters beyond the bifurcation, there is no attractor but the system's dynamics mimic its existence.



(a) (b)

Fig. 7. (a) Phase plane of the plankton-oxygen model (11)–(12) for parameters $A = 1.9$, $B = 1.8$, $c_1 = 0.7$, $c_2 = 1$ and $\eta = 0.2$. Black and red curves show the isoclines of Eqs. (11) and (12), respectively, the arrows show the direction of the phase flow. (b) The oxygen steady-state values (the high-oxygen branch and the low-oxygen branch, blue and red curves respectively) as functions of the oxygen production rate A. A decrease in A results in the two positive steady states merging and disappearing. For the values of A less than A_{cr} (shown by the vertical dashed line) there are no positive steady states.

As an instructive example, we consider the following model that described the oxygen-phytoplankton dynamics in the ocean [63–65]:

$$\frac{dc}{dt} = \frac{Au}{c+1} - \frac{uc}{c+c_2} - c, \tag{11}$$

$$\frac{du}{dt} = \left(\frac{Bc}{c+c_1} - u\right)u - \eta u, \tag{12}$$

(in dimensionless variables). Here c is the concentration of dissolved oxygen at time t, u the phytoplankton density, parameter A quantifies the rate of oxygen production in photosynthesis, B is the maximum phytoplankton per capita growth rate in the large-oxygen limit, η is the phytoplankton mortality rate, and c_1 and c_2 are half-saturation constants in the Monod-type kinetics. The first term in Eq. (11) describes the oxygen production, the second term parameterizes the oxygen uptake by phytoplankton as required for its metabolism (note that phytoplankton produces oxygen during the day but consumes it during the night), and the last term accounts for the oxygen loss due to its natural depletion (e.g. due to biochemical reactions in the water). In Eq. (12), the first term describes the logistic growth of phytoplankton and the last term stands for the phytoplankton mortality. For more details, see [63,64].

The phase plane of system (11)–(12) is shown in Fig. 7a. Considering A as the bifurcation parameter, it is readily seen that, for values of A not too small, there exist three steady states, i.e. the extinction state $(0, 0)$ and two positive steady states to which we refer as the high-oxygen state and the low-oxygen state. Stability of the steady states is readily seen from the direction of the phase flow (cf. the arrows in Fig. 7a): the extinction state and the high-oxygen state are stable nodes and the low-oxygen state is a saddle.

The position of the isoclines and hence the existence of the positive states depend on the parameters. It appears that a decrease in A eventually brings the system to a tipping point (see Fig. 7b). With a decrease in A, the first isocline moves upwards so that the two positive steady states move towards each other, merge for a certain critical value A_{cr} and disappear in a saddle-node bifurcation. For $A < A_{cr}$, the extinction state $(0, 0)$ is the only attractor of the system. However, since the solution of the system depends on the parameters continuously, for a value of A just slightly below its bifurcation value (in which case the isoclines do not intersect but come very close to each other), the properties of the phase flow and the corresponding vector field are very similar to what they are prior to the bifurcation. In particular, in the vicinity of the location in the phase plane where the equilibrium used to be for the subcritical values $A > A_{cr}$, the dynamics of the system are still largely determined by the vector field previously generated by the stable node; hence, the norm of the vector field is very low. Therefore, the system movement along the trajectories passing through that vicinity slows down considerably. As a result, beyond the tipping point the system's dynamics can mimic its behavior at the attractor over a considerable time (see Fig. 8). In the mathematical literature, this situation is referred

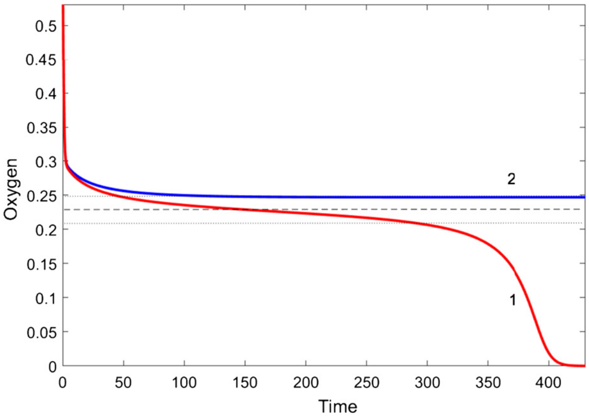


Fig. 8. Oxygen concentration vs time as described by model (11)–(12). Curve 1 (red curve) shows the solution obtained for parameters just beyond the tipping point (for $A = 1.38$, other parameters as in Fig. 7). The initial conditions are $c_0 = 0.8$ and $u_0 = 0.24$. Before going to extinction, the oxygen concentration converges to its ghost steady state value and remains in its vicinity (as shown by the dotted lines) for a considerable time: for the interval between $t \approx 30$ and $t \approx 300$, the change in the oxygen concentration is less than ±10% of its ghost steady state value. For comparison, curve 2 (blue curve) shows the solution before the tipping point (for $A = 1.9$) where it converges to a stable steady state.

to as a 'ghost attractor' [22,39,66] (or, somewhat more generally, slow manifold [67–69]) and the corresponding long transient as a ghost. Curve 1 in Fig. 8 shows a typical solution of the system (11)–(12) in this parameter range. After a fast decay of the initial oxygen concentration (approximately over the first twenty time units), the system enters the regime of slow dynamics: for the interval of about $t \approx 300$, the system stays in the vicinity of the ghost steady state value (shown by the dashed line) followed by a fast decay to extinction.

We therefore conclude that the relation between the tipping point and the long-term transient dynamics is the one between the cause and the effect. The bifurcation destroying the stable steady state – more generally, an attractor – is necessary to initiate the transition to another attractor. The long transient is a scenario of the transition where the system beyond the tipping point is hanging around its previous dynamical state (ghost state), so that its observed dynamics mimic the dynamics before the tipping point for a long time before any noticeable change occurs. When the parameter approaches its bifurcation value, the life span τ of the ghost-induced transient increases unboundedly. The time spent by the system's trajectory in the vicinity of the ghost steady state beyond a saddle-node bifurcation is typically scaled as a power law, $\tau \propto |A - A_{cr}|^{-\gamma}$, $\gamma > 0$, although the precise form can depend on the choice of the controlling parameter (see Appendix A). This result is generic; a similar long transient behavior due to a ghost attractor emerging from a saddle-node bifurcation is demonstrated by different models in life sciences, including models of embryonic development [24] and models of neural dynamics [22].

With regard to model (11)–(12), we mention here that it was developed in order to investigate the effect of global warming on oxygen production by ocean phytoplankton [63]. The dynamics of the system beyond the tipping point result in oxygen depletion which arguably can lead to a global ecological and humanitarian catastrophe [64]. In the corresponding real-world systems, in order to decrease the scale of the disaster or to avoid it altogether, the approach of the system to the tipping point would have to be closely monitored. The existence of the ghost steady state and the corresponding long transients could make this task challenging. Indeed, if the system is monitored on a time scale inconsistent with the inherent time scale of the transient dynamics, the ghost state may give a grossly misleading impression that the system is in a safe state.

Long transients resulting from a ghost attractor mechanism can also occur in the form of periodical oscillations. Periodical oscillations are ubiquitous in natural systems, arising either as a result of internal nonlinear interactions (e.g. between prey and predator) or due to strong external periodic forcing such as seasonality. Mathematically, a long-term periodical transient can occur via a fold bifurcation of stable and unstable limit cycles and creation of a narrow region (a channel) via which system trajectories eventually escape from the post-bifurcation ghost limit cycle (cf. [27]). This scenario was firstly applied by Pomeau and Manneville to model turbulence [70]. The corresponding population dynamics exhibit periodic oscillations for a long time, with almost constant amplitude, before suddenly switching to another regime. It can be shown that the lifetime of this transient behavior is scaled as $\tau \propto \epsilon^{-0.5}$, where ϵ is the width of the escape channel created after the bifurcation [27].

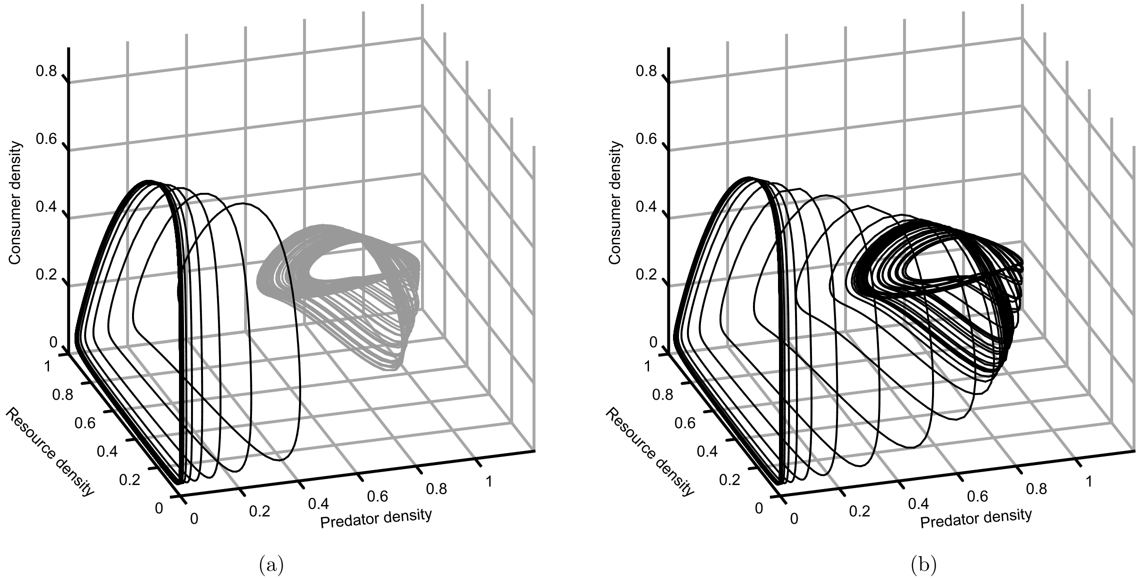


Fig. 9. Emergence of long term chaotic transients in a resource-consumer-predator system [61,71]. (a) For a subcritical value of the bifurcation parameter (carrying capacity), the system shows 'bistability' where the chaotic attractor coexists with a stable limit cycle; in particular, any trajectory started in a vicinity of the strange attractor will remain there. (b) The phase space after the bifurcation that turned the chaotic attractor into a ghost; any system's trajectory eventually converge to the stable limit cycle which is now the global attractor.

Apart from ghost steady states and ghost limit cycles, there are ghost chaotic attractors as well and they can arise in a number of ways [72]. For example, from dynamical systems theory it is well known that a cascade of period-doubling bifurcation would eventually result in chaotic dynamics (known as the Feigenbaum scenario [73]). In such systems the parameter set corresponding to the chaotic dynamics is extremely scarce in the sense that it contains no open intervals [74,75]. Parameter values corresponding to chaos are separated by 'windows' of parameter values where the dynamics are periodic. Unlike chaotic attractors, periodic windows are dense in the parameter space [73]. Correspondingly, a small variation of a parameter's chaotic value takes the system, via a tangent or a saddle-node bifurcation, to the window where the dynamics are asymptotically periodic. However, the dynamics do not change instantly; it takes a long time for the system to slowly converge to the periodical solution (cf. scenario (b) in our definition of long transients in Section 2). During this convergence time, the system's dynamics can be undistinguishable from the chaotic dynamics. The corresponding regime is called transient chaos. Therefore, a change in the bifurcation parameter destroys the chaotic attractor and create a chaotic ghost attractor where the dynamical variables behave chaotically for a long but finite time before settling into the final non-chaotic (periodic) state. An immediate important conclusion that apparently follows from the above is that, in real-world systems, transient chaos is likely to be more prevalent than permanent (asymptotic) chaos since the probability of finding parameters corresponding to asymptotic chaos is extremely small [72]. This message, however, should be taken with care, because the effect of noise, which is always present in empirical systems, can turn chaotic transients into permanent chaos (see also Section 4).

An example of a population dynamics model exhibiting a ghost chaotic attractor, and hence transient chaos, is given by a three-level trophic system consisting of a resource R, its consumer C and a predator P [61,71]. For certain parameter values, the dynamics of this system are known to be chaotic; Fig. 9a shows the corresponding 'strange' chaotic attractor in the phase space [71]. An increase in the resource carrying capacity destroys the strange attractor and brings the system to a periodic window. Population densities then demonstrate a long-term transient irregular behavior following the ghost of the strange attractor before the trajectory finally settles at the limit cycle (Fig. 9b). We mention here that long chaotic transients with similar properties are also observed in discrete-time systems [76].

Note that, with respect to the structure of the dynamical system's phase space and the corresponding behavior of the system's solutions, there is no essential difference between chaotic ghosts and chaotic saddles. In either case, the system can exhibit an apparently chaotic dynamics that last for a long but finite time before the system converges to a non-chaotic attractor. However, what makes the difference is the context in which chaotic ghosts and chaotic saddles are considered. Whilst the effect of chaotic saddles is associated with variable initial conditions but fixed parameter

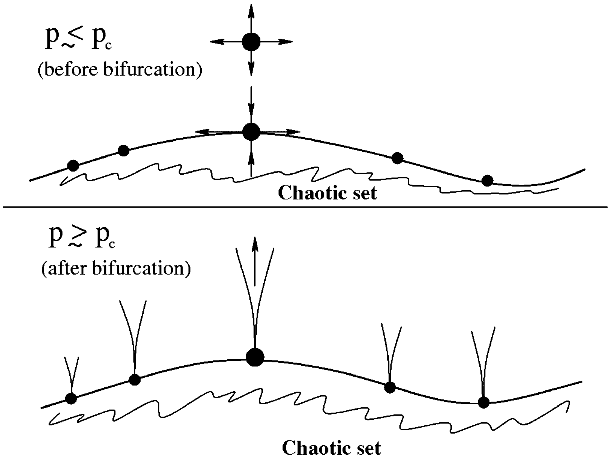


Fig. 10. Sketch of the dynamical mechanism of a chaotic supertransient emergence. Consider a nonlinear two-dimensional discrete-time dynamical system where p is a bifurcation parameter and p_c is its critical value. (top) For $p < p_c$, there is a chaotic attractor, the solid curve showing its basin's boundary. The two large black dots denote two unstable periodic orbits: one saddle-point on the attractor (with a stable and an unstable eigendirections) and another repeller (locally with a pair of unstable eigendirections) outside of the chaotic attractor. The small black dots on the boundary denote the preimages of the saddle-point. (bottom) At $p = p_c$, the saddle merges with the repeller, creating a narrow escaping channel near the saddle together with an infinite number of preimages of the channel for values of p slightly above p_c: a supertransient arises.

values (or parameter values varying over a range that does not include bifurcations), the concept of chaotic ghosts is used to describe the response of the system to a change in parameter values resulting in the bifurcation in the system's dynamics.

In systems with chaotic attractors, the lengths of transients can be especially large. In the literature, such transients (first discovered by Grebogi et al. [77,78]) are called supertransients. They usually arise as a result of the boundary crisis bifurcation when an unstable periodic orbit of a chaotic attractor collides with another unstable periodic orbit at the boundary of the attractor basin. Fig. 10 shows a schematic illustration of the dynamical setting in which a supertransient arises. Consider a two-dimensional discrete map. Let p be the bifurcation parameter and p_c its critical value, so that for $p < p_c$ there is a chaotic attractor. At the boundary of the attractor there is an unstable periodic orbit, which in two dimensions is typically a saddle-point with a stable and an unstable eigendirections. Outside of the attractor, there is a repeller on the basin boundary which locally has two unstable eigendirections. At the bifurcation point p_c, the saddle and the repeller merge, creating an infinite number of narrow "escaping" channels at the locations of the original saddle and all its preimages. Chaos is not sustainable any more; it becomes transient. Let T be the time (the number of iterations) required for a trajectory to travel through the channel away from the ghost of the chaotic attractor (in the vertical direction in Fig. 10). In order for this to happen, the trajectory must stay close to the entrance to the channel, i.e. approximately at the same location in the horizontal direction, consecutively for T iterations. For p slightly above p_c, the probability for a random trajectory on the original attractor to stay in the vicinity of the saddle for T consecutive iterations is approximately $P \propto e^{-\lambda T}$ where $\lambda > 0$ is the largest Lyapunov exponent. This estimate follows from the fact that, if the trajectory is in the channel, after T iterations it can be anywhere in the horizontal direction, so we obtain that $l e^{\lambda T} \propto 1$ (assuming that the size of the original chaotic attractor in the horizontal direction is on the order of unity) where l is a measure of the size of the escaping channel. Typically, the tunneling time depends on p algebraically [73] as $T \propto (p - p_c)^{-\gamma}$. Combining this relation with the expression for the probability P, we arrive at the following scaling law for the chaotic supertransient's average lifetime [77,78]:

$$\tau \propto \exp\left[k(p - p_c)^{-\gamma}\right], \tag{13}$$

where $\gamma > 0$ is the scaling exponent and $k > 0$ is a constant coefficient. Transient dynamics occur for $p > p_c$; as p approaches the critical value p_c, the transient lifetime grows unboundedly at a rate much faster than the power law.

In conclusion to this section, we briefly mention some empirical examples of long term transients linked to the ghost attractors. These include the switch from a macrophyte-dominated state to a turbid water state in freshwater lakes [79], the transition from coral to macroalgal dominance in Caribbean coral reefs [80,81], the shift from forage fish state to the state with dominance of large body benthic fish species in Scotian Shelf at Canada's East coast [82] and the shifts between populations of fish and invertebrates in watersheds in Western North Carolina after habitat's restoration [83]. In each of these cases, the transient dynamics were observed over a large number of generations (between five and fifty). We also mention that the existence of ghost attractors and their significance for the system's dynamics were reported in other life sciences, in particular in neuroscience where it was suggested that multistable ghost attractors could play a crucial role in brain functioning [84].

3.3. Slow-fast systems

Long transients can emerge in a population system where different populations have intrinsic time scales (as given by the generation times, the mortality rates etc.) of a different order of magnitude. The dynamical features related to the population with the shortest time scale are then referred to as 'fast' and those related to the population with the longest one as 'slow' [85]. Systems with these properties are ubiquitous in nature. The fast dynamics are often associated with the prey (resource) and the slow with the predator (consumer) [86,87], although opposite cases are well known as well (e.g. an insect-tree system [88,85]). One immediate real-world example where the prey's dynamics are fast and the predator's dynamics are slow is given by a plankton community where the phytoplankton growth can be 10-30 times faster than that of the zooplankton [89–91]. This is readily extended into a tri-trophic food chain as the fish feeding on the zooplankton would typically have intrinsic rates much smaller than the zooplankton [86]. Another example is given by an avian population feeding on insects where the ratio of the relevant characteristic times can be even larger depending on the biological traits of the species involved.

As an example of a slow-fast system, we consider a generic two-species model where the dynamics of species u are fast and the dynamics of species v are slow:

$$\frac{du(t)}{dt} = f(u, v, \epsilon), \qquad \frac{dv(t)}{dt} = \epsilon g(u, v, \epsilon). \tag{14}$$

Here $\epsilon \ll 1$ is a positive dimensionless parameter describing the 'difference' between the time scales. We mention here that in the theory of ordinary differential equations such systems are called stiff and they are known to present a considerable challenge for their numerical solution, exactly because of the existence of multiple time scales [92,93]. Note that, in original (dimensional) variables, the model does not necessarily contain a small parameter. However, a small parameter will inevitably appear explicitly, e.g. as the ratio of the growth rates, as soon as dimensionless variables are chosen. In more general terms, if the time scale of biological processes is considerably different for different species (see the examples above), an appropriate transformation of the original model is always possible that brings up a small parameter.

Introducing a rescaled time as $\tau = \epsilon t$, Eqs. (14) can be written as

$$\epsilon \frac{du(\tau)}{d\tau} = f(u, v, \epsilon), \qquad \frac{dv(\tau)}{d\tau} = g(u, v, \epsilon). \tag{15}$$

The time scale given by t is said to be fast whereas that for τ is slow. For any $\epsilon \neq 0$, systems (14) and (15) are equivalent. However, in the limit $\epsilon \to 0$ system (14) turns into

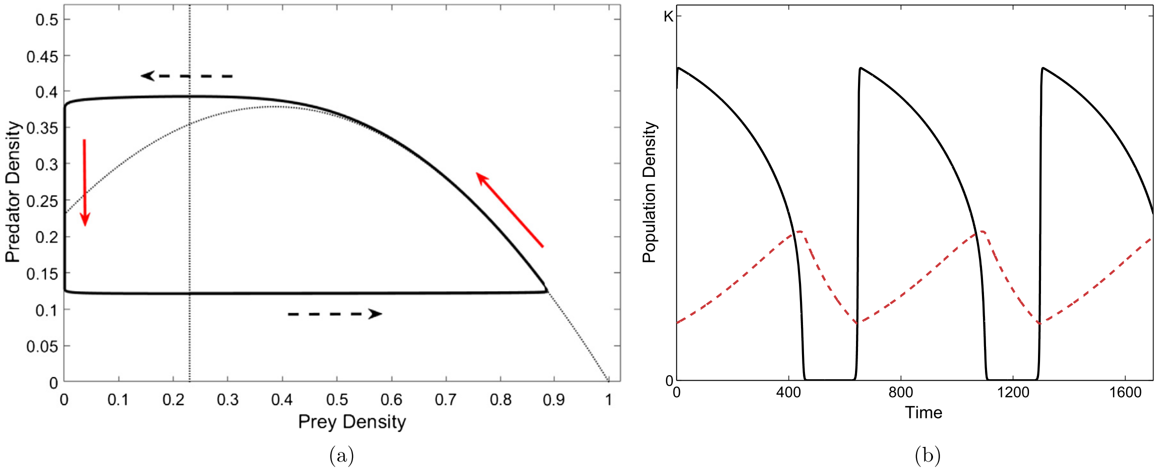
$$\frac{du(t)}{dt} = f(u, v, 0), \qquad \frac{dv(t)}{dt} = 0, \tag{16}$$

and system (15) turns into

$$0 = f(u, v, 0), \qquad \frac{dv(\tau)}{d\tau} = g(u, v, 0), \tag{17}$$

which are apparently different from the original systems. System (16) is sometimes called the fast system and system (17) is called the slow system, e.g. see [94]. For values of ϵ positive but small, the two limiting cases (16) and (17) give two different approximations to the original system, more specifically providing the (approximate) description of the system's dynamics for the fast and the slow phases, respectively.

In order to demonstrate the emergence of long transients due to the separation of fast and slow phases, we now consider the case where species u is the prey and species v is the predator. For the convenience of comparison to the non-stiff case, we consider functions f and g in Eqs. (16)–(17) to be the same as the right-hand sides in system (7)–(8) and focus on the case where the dynamics are oscillatory due to the stable limit cycle. For $\epsilon \ll 1$, the limit



(a) (b)

Fig. 11. Long term transients in a slow-fast prey-predator system. (a) The limit cycle in the phase plane of the system obtained for $\epsilon = 0.01$, all other parameters are the same as in Fig. 3a. Note the change in the shape of the cycle. The solid (red) and dashed (black) arrows indicate slow and fast dynamics, respectively. (b) The corresponding time courses of prey (solid black curve) and predator (dashed red curve).

cycle becomes deformed in a certain way (see Fig. 11a) so that different parts of the cycle correspond to slow and fast dynamics (indicated by solid and dashed arrows, respectively). During the fast phases the predator density remains approximately constant (cf. the second equation in (16)) and the corresponding parts of the cycle are aligned along axis u; during the slow phases the trajectory follows closely the isocline of the prey equation (cf. the first equation in (17)). Fig. 11b shows the corresponding time courses of the prey and predator densities. Arguably, each of the slow phases can be regarded as a long term transient dynamics. Almost-steady state dynamics of prey at low density accompanied by a gradual decrease in the predator density (as shown by the left-hand side of the cycle in Fig. 11a and the troughs of the solid curve in Fig. 11b) can go on for many generations of prey before suddenly changing to an outbreak in the prey population. The next long transient phase is a slow, gradual decrease in the prey population along with a slow increase in the predator population (the right-hand side of the cycle, a hump of the solid curve) before accelerating to a fast drop in the prey density. This sequence of slow and fast dynamics along the limit cycle repeats indefinitely. The natural scaling of the transient's lifetime in slow-fast systems is the inverse value of the timescales ratio ϵ, as readily follows from the definition of the slow time τ.

The shape of the limit cycle shown in Fig. 11a depends on the shape of the isoclines and hence on the properties of functions f and g. Correspondingly, the slow-fast dynamics can be analyzed via geometric methods [94]. For a different density dependence of the growth rates, the shape of the cycle can be different too. However, the splitting of the cycle to slow and fast phases (where slow phases are essentially the long term transients) is a generic property of slow-fast systems. In particular, it does not depend on the interpretation of u as prey (resource) and v as predator (consumer). System (14) was originally considered by Rinaldi at al. [85,95] as a model of insect-tree interaction where the insect species (consumer) has much higher growth rates compared to the trees (resource); see Fig. 12.

Note that it is not always possible to designate one of the species as fast and the other one(s) as slow and in fact the application of slow-fast systems is not restricted to this special case. In a somewhat more general situation, the slowness may refer to some of the processes but not necessarily to the population dynamics of a given species as a whole. In mathematical terms, it would mean that the right-hand side of at least one of the equations in the system (14) (or a similar model) does contain a small parameter, but not as a factor. Even more importantly, the concept of multiple time scales is by no means limited to the differential equations and can occur in other modeling frameworks, in particular in discrete-time systems [96]. The dynamics consisting of a sequence of fast and slow phases that is typical for stiff differential equations can turn into something more complicated, e.g. to a sequence of intermittent irregular oscillations of small and large amplitude. Fig. 13 shows an example of such dynamics observed in a discrete-time population model with control [96].

The existence of multiple time scales does not necessarily result in long transients being recurrent. Whether the long transient phase occurs periodically or happens only once depends on the properties of the system. One example

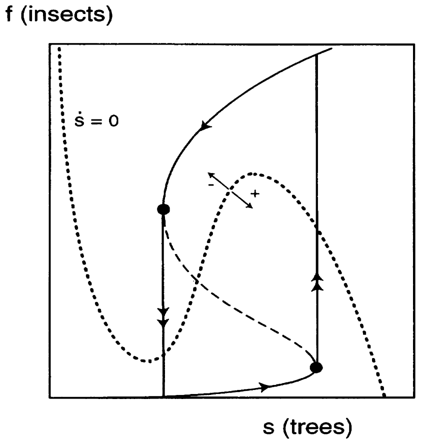


Fig. 12. The phase plane of the insect-tree population dynamics model [95]. The system's dynamics along the limit cycle split to slow phases (arrows) and fast phases (double arrows). Note that due to the different shape of the isoclines the shape of the cycle is different from that of Fig. 11a.

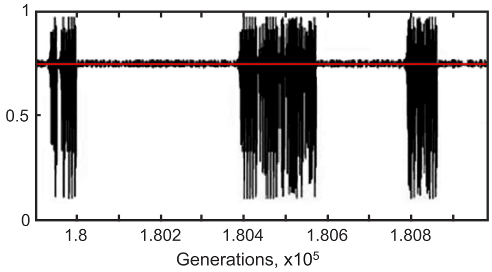


Fig. 13. Intermittent long term dynamics observed in a discrete-time single-species population model with a particular type of control. Each of the intervals where the oscillations are in the low-amplitude mode is a long transient. For details see [96].

of a unique, aperiodic long transient is given by the following two-species competition model:

$$\frac{du_1(t)}{dt} = r_1u_1(1 - b_1u_1 - a_1u_2), \qquad \frac{du_2(t)}{dt} = r_2u_2(1 - a_2u_1 - b_2u_2), \tag{18}$$

where u_1 and u_2 are the population densities, r_1 and r_2 are the per capita growth rates, and a_1, a_2, b_1 and b_2 are the coefficients describing the strength of intra- and interspecific competition. The difference of the time scales is quantified by the ratio $\epsilon = r_1/r_2$. The analysis presented above for model (14) readily applies to model (18). In case $\epsilon \ll 1$, the parts of the system's trajectory in the phase plane corresponding to fast dynamics are becoming approximately straight lines aligned in the vertical direction and the parts of the trajectory corresponding to the slow dynamics closely follow the relevant isocline; see Fig. 14a. Clearly, in this case the dynamics are not periodic; the stable steady state $(0, 1/b_2)$ (which is the only attractor in the system for these parameter values) is an ω-limit set of the system. The corresponding time courses of the population densities are shown in Fig. 14b. Unless the existence of the long transient is identified, and the population dynamics are observed only for a limited duration of time (say, over the first twenty units), this may send a grossly misleading message as species 2 apparently goes to extinction.

Thus, the slow-fast dynamics lead to the emergence of long transients but with somewhat different properties compared to ghosts and saddles/crawl-bys. Apparently, they are not directly related to the existence of NAIS (as with saddles) or to a bifurcation destroying an attractor (as with ghosts). In particular, the approximately constant values of some of the population densities observed during some of the slow phases may have little to do with invariant sets. However, a closer look reveals that the existence of NAIS does shape the properties of long transients significantly. The matter is that the slow dynamics can occur not only when the system moves along the attractive part of the critical manifold $f(u, v, 0) = 0$ (cf. the slow system (17)) but also along its repelling part [94,97]. The latter is related to the so-called canard solutions or canard cycles, which are a benchmarks of slow-fast systems. Combined effects of NAIS

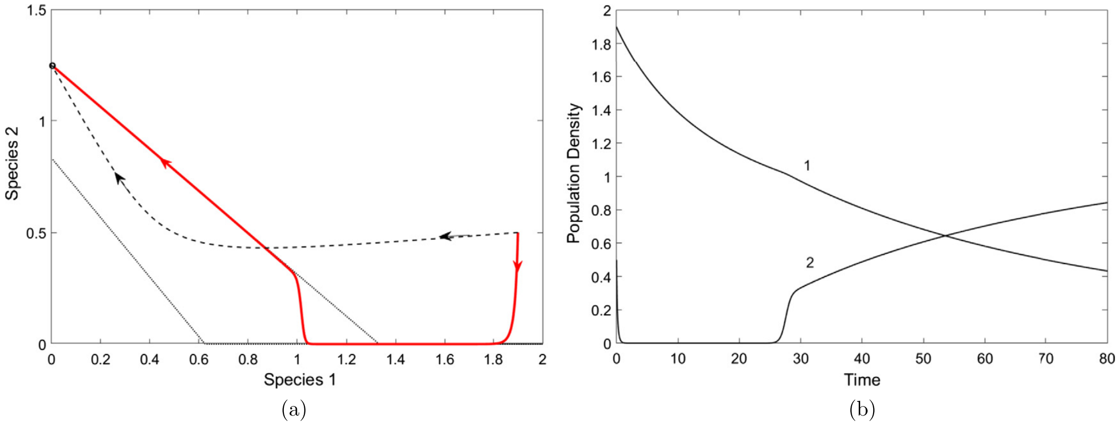


Fig. 14. Aperiodic long transients in a two-species competition system. (a) The phase plane of the system obtained for parameters, dashed (black) curve for $\epsilon = 1$, solid (red) curve for $\epsilon = 0.002$, the arrows show the direction of the phase flow. Dotted lines show the system's isoclines. (b) The corresponding population densities vs time, curves 1 and 2 for species 1 and species 2, respectively.

(e.g. saddles or unstable nodes) and fast-slow dynamics can result in new patterns of long transient dynamics such as "canard explosion" and the emergence of mixed-mode oscillations where small-amplitude and large-amplitude excursions alternate [94,97].

4. Effect of noise on transients

We have previously considered transient dynamics in fully deterministic models. In biological systems, however, there is always some noise both due to external and internal perturbations. Depending on the amplitude and the nature of noise, it can strongly affect transient dynamics. In particular, a supercritical noise can convert transient regimes in asymptotic ones.

Consider firstly a simple system exhibiting crawl-by dynamics near a saddle point (see Figs. 2, 3). The dynamics can be heavily affected by noise, causing substantially increased or reduced transient's length. In the case where the saddle point is located on a zero axis, stochasticity near this point may drive the species to extinction. On the other hand, noise can promote transient dynamics by setting possible initial densities such that the probability of settling in the basin of attraction of the stable manifold of the saddle point increases. This was empirically documented in the study of *Tribolium* where transients were observed in only some experiments and not the others despite the fact that the initial numbers of beetles in the experiments were close to each other [29].

Noise can be the main mechanism of formation of long transients when it causes random switching between two or more dynamical states; the system remains in each state for a long time (cf. Fig. 1b). Irregular switching of trajectories to various attractors due to noise is known as chaotic itineracy, attractor hopping or flickering [98]. Variation of the level of noise can largely affect the extinction time of a population, for example, by several orders of magnitude. This phenomenon is known as noise-delayed extinction and is due to interplay between system non-linearity, additive noise and variation of model parameters [99].

Stochastic perturbations can induce sustained transient oscillations around an equilibrium or a limit cycle that would be stable in the absence of noise. A well-known example of the transient dynamics generated by stochastic perturbation of a stable equilibrium is the population dynamics of Dungeness crab *Cancer magister* in USA west coast ports [100]. Using a combination of data analysis and model fitting to data it, is shown that observed chaotic-like oscillations are actually long transient relaxation dynamics occurring due to stochastic perturbations of a stable equilibrium. In another experimental setting, it was shown that random perturbations of the cyclic population dynamics can result in a chaotic-like behavior of the population density of *Tribolium* [101].

The noise can interplay with ghost attractors and promote recurrent long transients. In a simple case, where a channel of the ghost attractor is formed after fold bifurcation of limit cycles, the trajectory is kicked back to this channel from time to time due to noise resulting in a series of sustainable transients [27]. In more complicated settings, the recurrent transient dynamics will be chaotic.

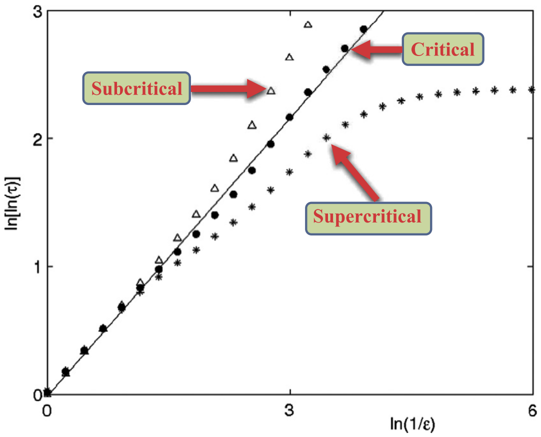


Fig. 15. Scaling laws of chaotic supertransient before and after the tipping point. The average lifetime of the chaotic transient is shown (in logarithmic coordinates) vs noise intensity shown for the subcritical ($p < p_c$, triangles), critical ($p = p_c$, filled circles) and supercritical ($p > p_c$, asterisks) cases. Adapted from [108].

On the other hand, a weak but supercritical noise can convert long chaotic transients into an asymptotic regime with chaotic dynamics. This phenomenon is known as noise-induced chaos [102–104], which is fundamental in nonlinear and statistical physics with significant applications in biology [105–107]. Noise-induced chaos can arise in periodic windows, where there is a periodic attractor and a chaotic NAIS lead to transient chaos. Noise can cause a trajectory to visit both the original attractor and the non-attracting chaotic set, resulting in an extended noisy chaotic attractor. Unlike purely deterministic systems, in models with stochasticity a chaotic attractor can occur in open sets in the parameter space [74,75]. This provides us with greater chances to observe chaotic attractors in real biological systems. Noise-induced chaos can arise in systems where a non-chaotic attractor coexists with a non-attracting chaotic set.

Noise can induce a supertransient for the parameter range where the chaotic attractor exists and the chaos is sustainable in the corresponding deterministic system. To see this, we again consider the setting in the upper part of Fig. 10 where the chaotic attractor still remains. From dynamical theory systems, it is known that such an attractor naturally embeds an infinite number of unstable periodic orbits. A subset of these orbits can be accessible to the basin boundary of the attractor in the sense that a path of finite length can be found that connects a periodic-orbit point to some point on the basin boundary. Likewise, there can be a subset of periodic orbits on the basin boundary that are accessible to the attractor. When noise is present, there can be a non-zero probability that two periodic orbits, one belonging to the accessible set on the attractor and another to the set on the basin boundary, can get close and coalesce temporally, giving rise to a non-zero probability that a trajectory on the chaotic attractor crosses the basin boundary and moves to the basin of another attractor. In this case, a transient chaos arises.

Due to noise, the channels through which a trajectory escapes from the chaotic attractor open and close intermittently in time. As in the absence of noise, because of chaos, the probability of escape is extremely small because escaping through the channel requires the trajectory to remain in a small vicinity of the opening of the channel for a finite amount of time, which is an event with extremely small probability. In this sense, the channel must be "super" narrow [77,57], leading to a supertransient. The creation of the channel by noise and the stochastic dynamics in the channel are the key to understanding the noise-induced transient behavior. Thus, noise creates a link between the two different mechanisms of emergence of transients, i.e. ghost attractors and saddles, the resulting supertransients being an interplay of these mechanisms.

Adding noise to a system with a strange attractor can result in the emergence of very long chaotic transients [109]. Fig. 15 shows the dependence of lifetime of transients on the amplitude of noise. Here the underlying deterministic system has a chaotic attractor before the tipping point, i.e. for $p < p_c$, at $p = p_c$ the chaotic attractor turns into a chaotic saddle so that for $p > p_c$ chaotic dynamics are transient. In the presence of chaos, there is a non-zero probability of the system leaving the basin of the attractor, hence the sustainable chaotic dynamics become transient. Interestingly, the effect of noise can be distinct in different parameter regions, i.e. for $p < p_c$, for $p = p_c$ and $p > p_c$, which is shown in the figure. As such, we divide the parameter interval into two regimes: subcritical and supercritical;

for each region the scaling law for the average life time is different. In particular, in the case of weak noise the transient lifetime shows a much faster rate of increase described by a double-exponential with algebraic law (see Eq. (20)).

A rigorous mathematical analysis led to the following results [109,108].

- At the critical point ($p = p_c$), noise induces transient chaos with the average lifetime obeying the normal superpersistent scaling law:
$$\tau \propto \exp(C\varepsilon^{-\gamma}), \tag{19}$$
where $C > 0$ is a constant and $\gamma > 0$ is the algebraic scaling exponent in the exponential dependence of τ. While the scaling law is general, these constants are system dependent.
- In the subcritical regime ($p < p_c$) where a chaotic attractor exists in the absence of noise, for relatively large noise (e.g., $\varepsilon > \varepsilon_c$, where ε_c depends on $|p_c - p|$ and $\varepsilon_c \to 0$ as $p \to p_c$), the average lifetime of the noise-induced chaotic transients obeys the normal scaling law (19). However, for weak noise ($\varepsilon < \varepsilon_c$), the average lifetime scales with the noise amplitude ε according to the following double exponential and algebraic law:
$$\tau \propto \exp[K_0 \exp(K_1\varepsilon^{-\gamma})], \quad \text{for } p < p_c, \tag{20}$$
where $K_0 > 0$, $K_1 > 0$, and $\gamma > 0$ are constants. Because of the double exponential dependence and the algebraic divergence for small noise, the corresponding transient's lifetime can be significantly longer than that given by the normal superpersistent scaling law (19). Such transients are called "extraordinarily-superpersistent chaotic transients" [109].
- In the supercritical regime ($p > p_c$) where there is already a chaotic transient, the lifetime has no dependence on the noise amplitude if it is small. However, for relatively large noise, the lifetime decreases following the normal superpersistent scaling law (19). Thus, in this case the chaotic transient lifetime in the presence of noise can be significantly shorter than that in the absence of noise.

The reported supertransients caused by noise as well as extraordinary supertransients may play a significant role in observing chaotic behavior in empirical systems since the models predict large parameter ranges where chaotic behavior can be observed, whereas in purely deterministic models chaos is often structurally unstable.

5. Transients in spatial systems

In general, spatial systems tend to exhibit more complicated dynamics than their nonspatial counterparts. Indeed, in the context of the dynamical systems theory, a spatial system has higher dimensionality than the corresponding nonspatial one, and hence intuitively can be expected to have a greater dynamical complexity. A straightforward example is given by a space-discrete system of N coupled patches where each patch is inhabited by a population community of M interacting species; obviously, the dimension of this system (e.g. described by coupled ODEs or by coupled maps) is $M \times N$. Space-continuous systems can be thought of as higher dimensional systems too. The range of situations where long transients are observed in spatially extended systems is broader and the transients themselves can be more complex. Although nonspatial counterparts create a 'skeleton' for understanding long transients in spatial systems, the existence of spatial dimension(s) affects the properties of long transients significantly, for instance, by changing the scaling laws (i.e. the dependence of the transient's lifetime on the controlling parameters). Moreover, as we will show below the spatial dimension brings in new types of long transients that simply do not exist in the nonspatial systems.

Long transients are ubiquitous in spatial systems (albeit restricted to a certain parameter range) and occur both in space-discrete and space-continuous settings. The properties of the long transients as well as the mathematical models and methods that are used to study them are, however, somewhat different in discrete and continuous space. Thus, we consider these two cases separately.

5.1. Spatially continuous systems

Ecologically meaningful mathematical frameworks commonly used to model population dynamics in continuous space are given by partial differential equations and integral-difference equations. The type of transient dynamics and

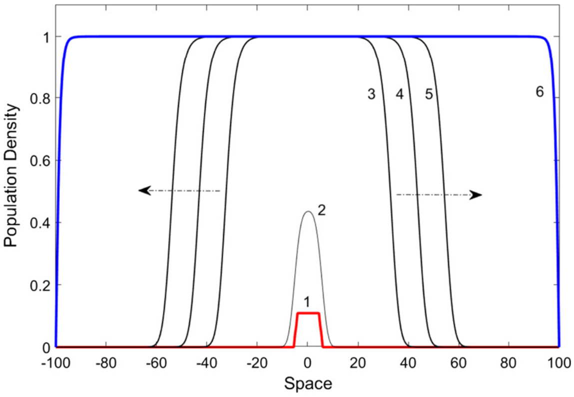


Fig. 16. Transient spatiotemporal dynamics of an alien species invasion in a large yet finite spatial domain described by the scalar reaction-diffusion equation with the logistic growth. At the boundaries of the domain, the zero-density Dirichlet boundary conditions are used. A finite initial population distribution (red line) fast develops into the propagating front (cf. curves 3-5) that travels with a constant speed without changing its shape until it reaches domains boundary. Front propagation is therefore a long transient. Blue curve 6 shows the stationary large-time asymptotics.

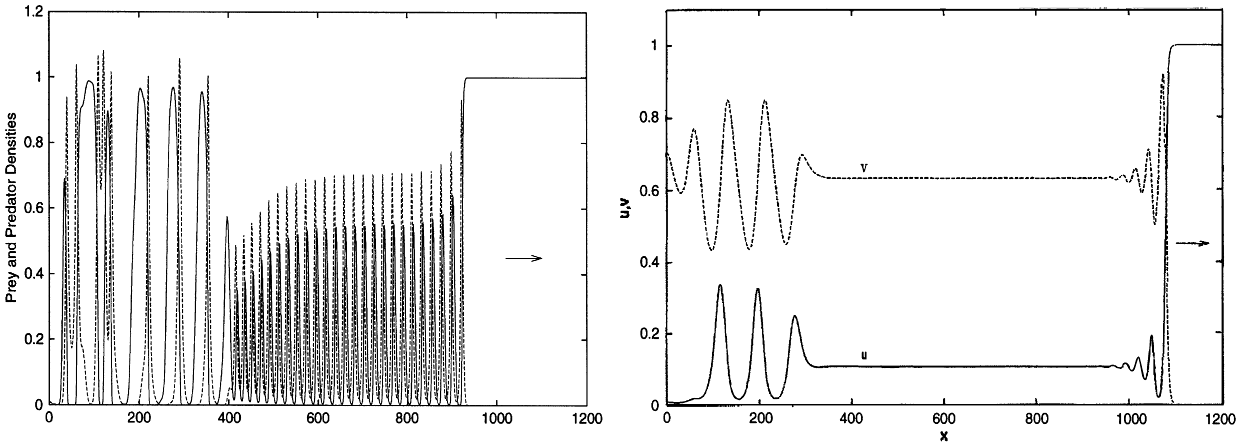
its properties depend on the initial conditions, and hence on the ecological context in which the population dynamics are considered. Two different cases are given by the compact initial conditions where at least one of the species is initially present only in a finite area or small subdomain, and by the distributed initial conditions where all species are initially present everywhere in the spatial domain.

Compact initial conditions. This type of the initial species distribution arises naturally in modeling biological invasions [110,111]. The evolution of compact initial condition typically leads (unless the introduced population is driven to extinction by a strong Allee effect [112]) to the formation of a traveling population front propagating away from the place of the species introduction. As an illuminating example, Fig. 16 shows the spread of invading species described by a single-species reaction-diffusion model. Ahead of the front the species is absent, behind the front it is present at considerable density (not necessarily uniform in a more realistic case, see below). The regime of traveling population wave is a common property of growth-dispersal models [111]. In an unbounded space, the traveling population front is the asymptotic dynamics of the system. In a bounded domain, the traveling front propagation is not the asymptotic dynamics but a long transient. The front stops and converges to the actual large-time asymptotics when it reaches the domain boundary (i.e. the limits of the species range); see the thick blue curve in Fig. 16. The duration of the traveling front propagation therefore depends on the spatial extent of the domain as $\tau \propto L/c$ where L is the domain's length in the direction of the front propagation and c is the speed of the front. This situation is different from that observed in the nonspatial systems. In nonspatial systems, the duration of long transient is an inherent property of the dynamics, i.e. of the equations. In the spatial systems, whilst the traveling wave speed is an inherent property of the dynamics, the domain length is an external factor. Obviously, for the same system (e.g. the same invader in the same population community) but in a different spatial domain the duration of the traveling wave regime can be very different depending on the domain's spatial extent. The dependence on the system size is a specific property of spatial systems.

Note that the population distribution behind the front depends on the interaction of the invading species with other species or agents, e.g. with the native species or endemic infection. In a more realistic model that accounts for these interactions, and hence consists of a system of coupled reaction-diffusion equations, the population density distribution in the wake of the front can become heterogeneous or even patchy due to the self-organized pattern formation [113,114]. In this case, the spread of the invading species usually takes place through the propagation of a sequence of traveling waves. Fig. 17 shows two examples of this dynamics obtained in the following 1D spatial prey-predator system:

$$\frac{\partial u(x,t)}{dt} = D_u \frac{\partial u^2(x,t)}{\partial x^2} + f(u,v), \qquad \frac{\partial v(x,t)}{dt} = D_v \frac{\partial v^2(x,t)}{\partial x^2} + g(u,v), \tag{21}$$

where D_u and D_v are the diffusion coefficients and functions f and g are the same as in (7)–(8). In the case shown in Fig. 17a, the traveling population front is followed by a wavetrain of almost periodical oscillations propagating with the same speed and without changing is shape – effectively, a traveling wave of a complicated structure. In the



(a) (b)

Fig. 17. Invasion of predator into the space occupied by prey (described by a 1D reaction-diffusion system) through a succession of traveling population waves. (a) Propagation of the population front is followed by a band of nearly-periodic wave which is followed by the onset of irregular oscillations [115]. (b) Propagation of the population front is followed, after a few promptly decaying oscillations, by the transient regime of the 'dynamical stabilization' (the formation of a plateau corresponding to an unstable steady state) [115,117].

wake of the wavetrain, chaotic spatiotemporal oscillations develop [113]. The succession of waves shown in Fig. 17b is even more curious. In this case, in the wake of the population front, after a few promptly decaying oscillations the population densities converge to a spatially uniform distribution corresponding to the coexistence steady state of the nonspatial system. Interestingly, for these parameter values the steady state is unstable. The formation of the unstable plateau in the wake of the propagating front is called the dynamical stabilization [115]. Behind the plateau, the spatiotemporal chaos eventually develops; however, since the boundary separating the plateau from the chaotic oscillations moves very slowly [116], usually much slower than the leading population front, the length of the plateau can grow with time and reach a significant size. Extension of system (21) onto 2D space shows similar properties [117]. The mathematical theory of dynamical stabilization in reaction-diffusion systems (which relates it to the so-called convective stability, i.e. the stability of solutions in the moving reference frame) predicts that, in an unbounded domain, the length W of the plateau grows unboundedly as a scaling law, $W \propto p^{-\gamma}$, where p is a controlling parameter [118]. In a bounded domain, as the area occupied by the chaotic oscillations grows with time, eventually the plateau is getting destroyed when chaos occupies the whole domain [116].

Arguably, the regime of dynamical stabilization can be regarded as a long transient. An observer with a limited information about the spatial dynamics of the system (a situation which is not uncommon in ecology), ultimately in possession of the data collected at just one fixed spatial location, would apparently arrive at a conclusion that the alien species, after experiencing some fluctuations of decreasing magnitude, reaches a stable steady state. However, this conclusion would be obviously wrong and any management decisions based on it would likely be inefficient and largely irrelevant.

The formation of transient spatiotemporal patterns in the wake of the propagating population front, such as a wavetrain of regular spatiotemporal oscillations or the dynamical stabilization (see Figs. 17a and 17b, respectively) is not limited to the prey-predator system but in fact is a generic property of a reaction-diffusion system in the parameter range where its nonspatial counterpart possesses an unstable positive steady state (unstable focus) [119]. As another example of an ecologically meaningful model exhibiting this type of long transient dynamics, we consider a three-species system with cyclic or near-cyclic competition [45,46]. In this system, in the 1D space the compact initial conditions develops into a sequence of traveling fronts followed by the dynamical stabilization and/or a nearly-periodical wavetrain and, eventually, spatiotemporal chaos [120]. In the 2D and 3D space, the species spread follows a largely the same scenario but exhibiting more complicated spatial patterns, e.g. where the spread takes place via growing ice-cream-like, cone-shaped area (see Fig. 18). The regular pattern developing behind the propagating vertex of the cone is essentially long transient dynamics. In the wake of the propagating regular pattern, chaotic oscillations develop, so that eventually the system is invaded by spatiotemporal chaos, which is the asymptotic regime of system's dynamics [121].

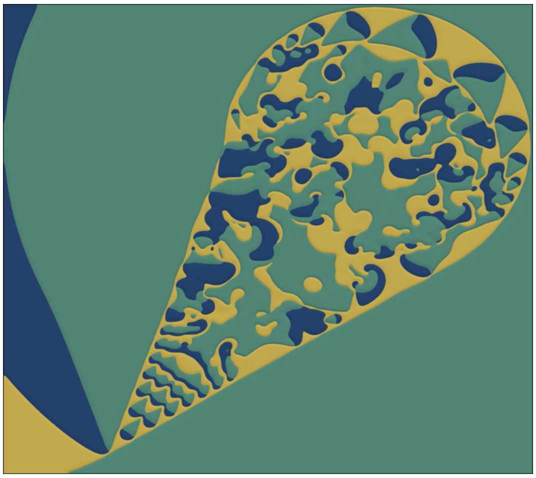


Fig. 18. Snapshot of the species distribution over space in a three-species competition system described by a 2D reaction-diffusion system [121]. Different colors show that areas dominated by different species. The species spread takes place through the growth of the cone-like area. Behind the propagating vertex of the cone, a transient regular pattern is formed.

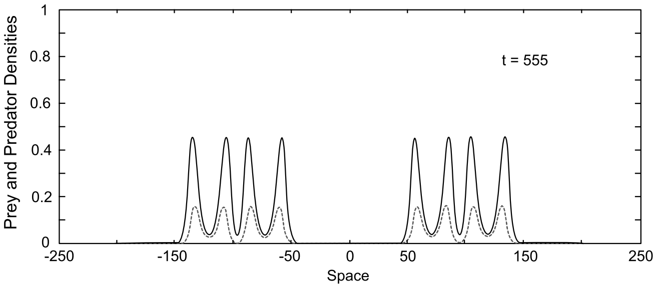


Fig. 19. Transient regime of pattern formation in a reaction-diffusion prey-predator system with the strong Allee effect [122]. Compact initial distribution of a small size centered around the origin develops into a patchy distribution that occupies considerable space and mimics a sustainable regime over a considerable time before suddenly collapsing to extinction.

Spatial systems can also exhibit long transient dynamics that follow the generic scenarios identified for nonspatial systems (see Section 3). In particular, long transients due to ghost attractors emerge for parameter values close to the parameter range of sustainable dynamics [122]. The transient regime than mimics the corresponding asymptotic regime. For instance, the evolution of initial population distribution can result in the formation of spatiotemporal patterns (cf. Fig. 19) that persist for a remarkably long time before collapsing to extinction. During that time, the properties of the dynamics are practically indistinguishable from the prototypical, truly asymptotical, sustainable dynamics. We emphasize that, contrary to the case of front propagation discussed above, in the case of transient patterns emerging from compact initial conditions the transition to the large-time asymptotics occurs due to the inherent properties of the dynamics, not due to the effect of the domain boundaries. The domain size has no effect on the transient's lifetime. The closer parameter values are to the boundary of the parameter range of sustainable dynamics (i.e. to their bifurcation value) the longer the duration of the long transient is, exactly as it happens in case of ghost attractors in nonspatial system.

Distributed initial conditions. In case of distributed initial conditions, population fronts are not directly relevant but population waves of other types can emerge. The type of population dynamics show stronger dependence on the properties of the initial distribution than in case of the compact initial conditions. If the local (nonspatial) dynamics are oscillatory (e.g. because of the Hopf bifurcation), the initial conditions that include large gradients lead to the onset of spatiotemporal chaos following the 'wave of chaos' scenario [116,123]. At an early stage of the dynamics, a subdomain appears with chaotic population oscillations inside but nearly-periodic oscillations outside (see Fig. 20), the two dynamical regimes being separated by a narrow self-organized interface. In the course of time the chaotic

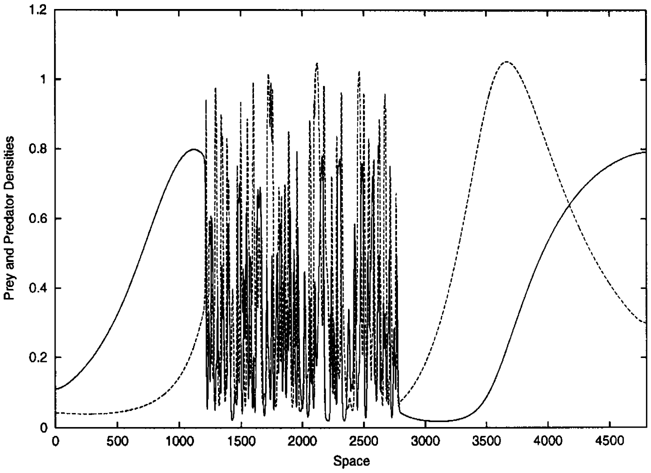


Fig. 20. Transient regime of the 'wave of chaos' propagation in a spatial prey-predator system [116]. The regular mode of the system's dynamics is eventually displaced by the chaotic mode but the two modes can coexist for a very long time.

domain grows in size, so that eventually chaos occupies the whole domain. For the diffusive prey-predator system, it can be shown that the self-organized interface propagates with a constant speed estimated as $v \propto (\mathrm{Re}\,\lambda)^{1/2}$ where $\mathrm{Re}\,\lambda$ is the real part of the eigenvalues of the system linearized in the vicinity of the positive steady state [116]. Thus, for a given length of the domain, the lifetime of the transient regime of the wave of chaos propagation depends on the parameters as $\tau \propto (\mathrm{Re}\,\lambda)^{-1/2}$. An observer monitoring the population dynamics at a fixed location in space, originally positioned outside of the chaotic domain, would have perceived long-term regular, nearly-periodic dynamics suddenly changing to chaos without any apparent reason.

On the contrary, a smooth, small-gradient initial condition does not lead to the onset of chaos even if the local dynamics are oscillatory, but the system exhibits a long transient of a different kind. At the early stage of the dynamics, the initial conditions quickly evolve to a smooth large-amplitude spatial pattern (similar to what is shown in the right-hand side of Fig. 20 but now occupying the whole domain), with local oscillations being nearly-periodic in time. However, this pattern is not sustainable and shows an extremely slow convergence to, in the large-time limit, the spatially uniform distribution [116].

Long transients apparently caused by a chaotic saddle have been observed in a three-species reaction-diffusion model of the plankton-oxygen dynamics, i.e. the spatial extension of model (11)–(12) accounting also for the effect of zooplankton [64]. In a certain parameter range (for intermediate values of the oxygen production rate A if considering it as a controlling parameter), the system exhibits sustainable spatiotemporal chaos. Once the value of the bifurcation parameter changes to a higher, over-critical value, chaos is not sustainable in the large-time limit but can persist over a long time before the system collapses (see Fig. 21). During this interval of the quasi-sustainable long transient dynamics, both the time-dependence of the average densities (cf. Fig. 21) and the spatial patterns (not shown here for the sake of brevity) show qualitatively the same features as in the sustainable dynamics for under-critical parameter values.

The average lifetime of long transients in space-time-continuous systems, in particular in reaction-diffusion systems, is known to increase along with an increase in the size of the domain L. Depending on the type of the nonlinearity, i.e. the density-dependence of the population growth rate (reaction), the corresponding scaling can be described either by a power law [124]:

$$\tau(L) \propto L^{\gamma_1}, \tag{22}$$

or by an exponential function:

$$\tau(L) \propto \exp\left(aL^{\gamma_2}\right), \tag{23}$$

where γ_1 and γ_2 are positive exponents and a is a coefficient. In the physical literature, the corresponding dynamics are referred to as Type-I and Type-II transients, respectively [124].

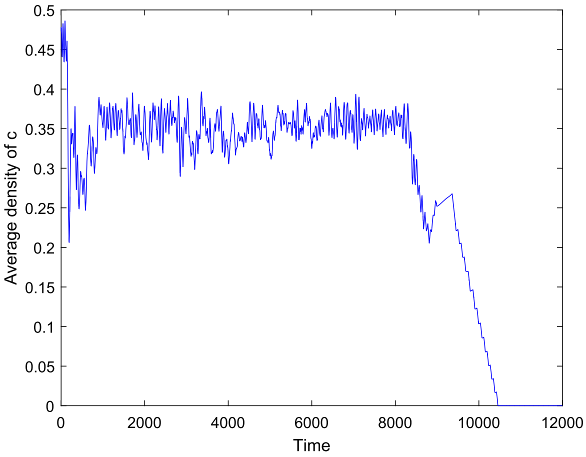


Fig. 21. Long-term transient dynamics of spatially-average oxygen concentration in a marine ecosystem described by a three-species reaction-diffusion model [64]. At small time, the system is in the sustainable regime of spatiotemporal chaos. At time $t \propto 100$, the value of the controlling parameter changes to an over critical value where the system is not sustainable in the large-time limit; however, the dynamics mimic the sustainable regime over a remarkably long time before experiencing a fast transition to extinction.

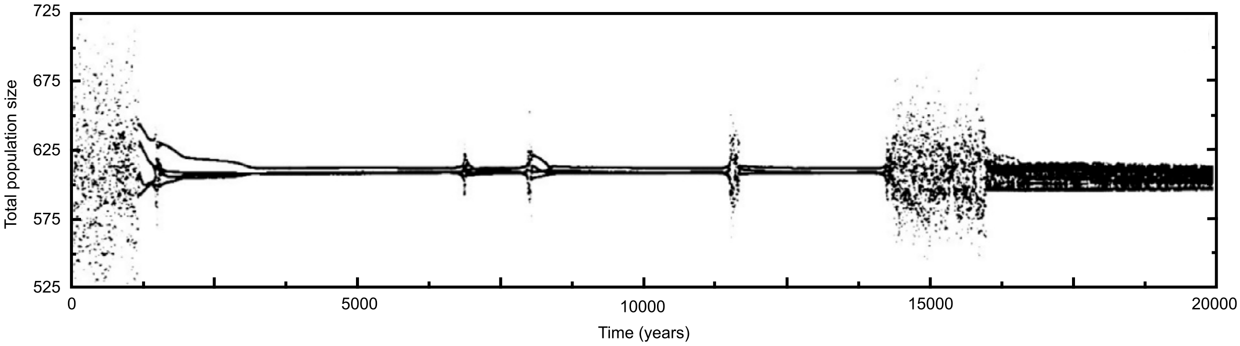


Fig. 22. Long transients in the space-continuous discrete-time model (24). From [125].

We emphasize here that long transients are not only a property of the reaction-diffusion framework. Long-term transient dynamics were observed in a space-continuous discrete-time model described by the following integral-difference equation [125]:

$$u(x,t+1) = \int_0^L g(x-y)F(u(x,t))dx. \tag{24}$$

where $u(x,t)$ and $u(x,t+1)$ are the population density distributions in generation t and generation $t+1$, respectively, function F describes the rate at which the offsprings are produced in generation t, function g is the probability for the offspring to travel to a new location x from the release location y, and L is the size of the spatial domain. We mention here that integrodifference equations are commonly used to model the population dynamics of stage-structured populations, in particular, in the case where the reproduction stage and the dispersal stage are clearly different [126, 127].

Using the Ricker map for F and the normal distribution for g and assuming random initial population distribution, it has been shown in numerical simulations that model (24) exhibits a variety of long transients. As an example, Fig. 22 shows the spatially averaged population density as a function of time. It is readily seen (for more details see [125]) that long intervals of periodic dynamics alternate with long intervals of chaotic dynamics (lasting hundred or event thousands of generations) before the system finally settles down on the attractor which, depending on parameter values, can be either periodic or quasi-periodic. The lifetime of chaotic transients depends on the parameter values; in particular, for randomly chosen parameter values long chaotic transients are only observed in a certain percentage of simulations [128].

5.2. Spatially discrete systems: coupled maps

Spatial models that are discrete both in time and space arise as a natural modeling framework to describe the dynamics of a population with non-overlapping generations dwelling in a fragmented habitat consisting of an array of patches coupled by dispersal. Mathematically, they are given by coupled map lattices (CML). As a paradigmatic model, we consider the population dynamics on a 2D rectangular lattice Ω consisting of $N_x \times N_y$ nodes:

$$\Omega = \{(x_j, y_l),\ j = 1, \dots, N_x,\ l = 1, \dots, N_y\}. \tag{25}$$

In case each of the nodes is inhabited by a community of M interacting species, the dynamics are described by the following system:

$$u_k^{i+1}(j,l) \ = \ (1-\mu_k) F_k\left(\mathbf{u}^i(j,l)\right) + \sum_{\hat{j},\hat{l} \in V_{jl}} \left(\frac{\mu_k}{s_V}\right) F_k\left(\mathbf{u}^i(\hat{j},\hat{l})\right), \quad k = 1, \dots, M. \tag{26}$$

Here $\mathbf{u}^i(j,l) = \left(u_1^i(j,l), u_2^i(j,l), \dots, u_M^i(j,l)\right)$ is a vector made of the population densities of all species at node (j,l) and discrete time i (e.g. counted in generations), and F_k is the number of offsprings produced by species k during the reproduction stage. Coefficients μ_k quantify the strength of dispersal coupling: it is the fraction of the population size of species k that leaves the given node during the dispersal stage to migrate to the neighboring nodes. Thus, the first and second terms in the right-hand side of (26) describe the migration out of and into the given node, respectively. The multiplicity of the nodes V coupled by dispersal is sometimes called the dispersal stencil; s_V is the number of nodes in the stencil. Depending on the properties of dispersal, e.g. short distance vs long-distance, V can include only close neighboring nodes or neighboring nodes and more distant nodes. In the former case, as two immediate options V can include either four or eight neighboring nodes. In Eq. (26), we have assumed that all nodes in the dispersal stencil contribute equally to the inbound population, which is arguably a reasonable assumption in the case of short-distance dispersal (where only close neighbors are coupled) but not necessarily in the case of long-distance dispersal.

Depending on the number of species M and the parametrization of reproduction rates F_k, model (26) is known to exhibit a variety of spatiotemporal patterns including spiral patterns, spatial chaos and spatiotemporal chaos as its large-time limit [129–131]. In the case where model (26) describes a prey-predator system, long transients due to ghost limit cycles and ghost chaotic attractors were observed [131].

A special yet instructive case of CML is given by a 1D string of single-species nodes (patches) where only close neighbors are coupled:

$$u_j^{i+1} = (1-\mu) F(u_j^i) + \frac{\mu}{2}\left[F(u_{j+1}^i) + F(u_{j-1}^i)\right], \qquad j = 2, \dots, N-1. \tag{27}$$

In this case, the dispersal stencil obviously consists of only two points. The value of the scalar state variable u at the furthermost nodes in the string, i.e. for $j = 1$ and $j = N$, are defined by the boundary conditions.

Model (27) has been studied intensively in physical applications as a model of turbulence [133,134] and it was shown that its spatiotemporal dynamics can exhibit long-term transient chaos. The corresponding spatial pattern consists of irregularly alternating domains (groups of nodes) with chaotic or non-chaotic local dynamics (see Fig. 23). Because the lifetime of these chaotic transients can be very long, they are sometimes referred to as super-persistent transients or supertransients. As well as in space-continuous systems, the average lifetime of the transients depends on the system size which, in case of a 1D string (27), is measured in the number of nodes N. The dependence of the lifetime on the system size can be different for different strength of dispersal coupling. There are two critical values of the coupling strength, say μ_0 and μ_c. For $\mu_0 < \mu < \mu_c$, the lifetime is scaled with the system size as a powers law and for $\mu > \mu_c$ as an exponential, that is

$$\text{(a)}\ \ \tau(N) \propto N^{\gamma_1} \quad \text{and} \quad \text{(b)}\ \ \tau(N) \propto \exp\left(a N^{\gamma_2}\right), \tag{28}$$

hence corresponding to Type-I and Type-II supertransients, respectively [124].

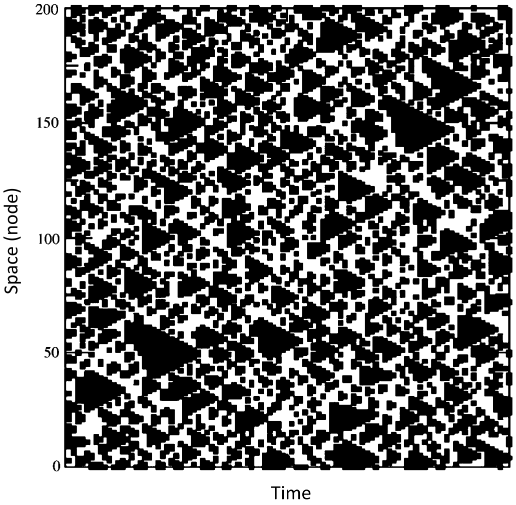


Fig. 23. Typical spatiotemporal plot of the dynamics of system (27) during a long-term transient chaos. Vertical axis for space (node number), horizontal axis for time. White color shows domains with local chaotic dynamics, black color shows domains with local non-chaotic (periodic or quasi-periodic) dynamics. In the course of time, the transient intermittent chaotic structure eventually disappears, so that, in the large-time limit, the dynamics of the system at all locations in space become periodic. From [132].

The evolution of the two types of supertransients with time is different too [135]. For Type-I supertransients, dynamical invariants such as the Lyapunov exponents and entropies gradually decrease with time. Type-II supertransients are, in contrast, statistically steady over a long period of time, i.e. the average characteristics of the chaotic state are time-independent, and at the end of the transient's lifetime, the transition to the ω-limit attractor is rather abrupt. We mention here that these two types of behavior are paradigmatic for the long-term transients; see the definition in Section 2.

6. Transients in systems with time delay

In all previous examples, it was assumed that reproduction, maturation, competition, predation, etc., are instantaneous processes, i.e. the rate of the corresponding change in the population density at a given moment depends on the value of the population density at the same moment [137–140]. However, in real biological systems this is not always true and many processes are subject to time delay [141,142]. The question therefore arises as to how the presence of time-delay in the system may affect the existence of long transients and their lifetime. Although this issue is relatively poorly understood, several case studies are available from the literature and some inferences can be made based on semi-heuristic arguments. In the context of the dynamical systems theory, the presence of a time delay in a model is known to increase its dimensionality and hence to enhance its dynamical complexity. It can therefore be expected that long transients are likely to be even more common in systems with time delay than they are in instantaneous systems.

It was demonstrated in several studies that a sufficiently long time delay can result in the emergence of long transients [37,143]. Considering the value of the delay (say, ζ) as a natural controlling parameter, it has been shown in simulations using a nonspatial time-continuous single-species model with the strong Allee effect that the lifetime of the emerging long transients is proportional to delay, $\tau \propto \zeta$. In another study [37], it was shown that delay-caused long transients are similar to those caused by ghost attractors (e.g. see Fig. 1a). However, we mention here that this apparent similarity should be regarded with care: as systems with time delay are usually infinitely-dimensional [142, 144] (except for a special choice of a distributed delay), the phase space arguments used to visualize ghost attractors become largely irrelevant.

The effect of time delay on the emergence of long transients in spatial systems can also be understood, at least in some cases, through the increase in the system dimensionality. For instance, it is well known that the evolution of compact initial conditions in a scalar (single-species) reaction-diffusion system can only result in monotonous traveling fronts (cf. Fig. 16). More complicated regimes and the corresponding long transients such as periodical wavetrains and dynamical stabilization can only occur in a system that includes two or more species. The presence of

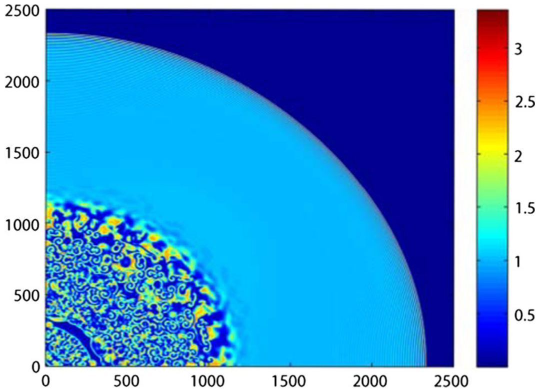


Fig. 24. Snapshot of the population distribution obtained in a space-time-continuous single-species model with time delay. At the beginning, the population is only present in a small area around the origin, i.e. in the bottom-left corner of the domain. The evolution of the initial condition results in the formation of the traveling population front, behind the front the unstable plateau (shown by light-blue color) emerges as a result of dynamical stabilization. The plateau is a transient dynamical structure. In the wake of the unstable plateau, spatiotemporal chaos develops. From [136].

time delay, however, makes these transient regimes possible already in a single-species system [136]; an example is shown in Fig. 24.

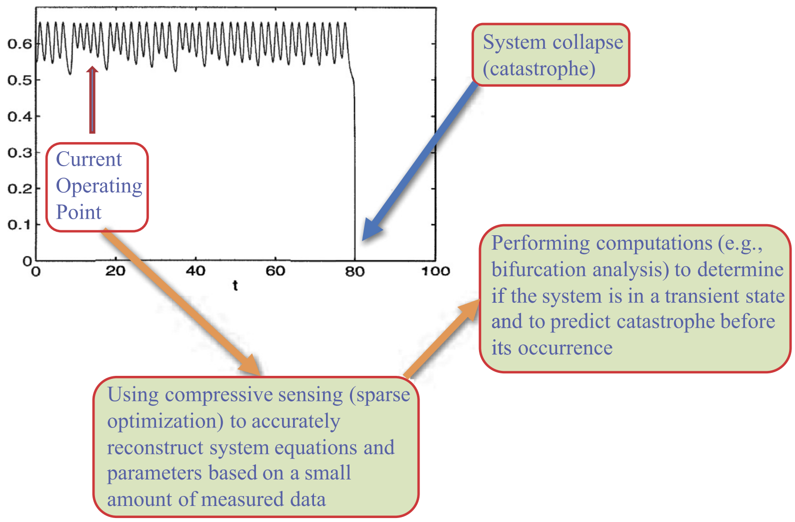
7. Anticipating transient-related regime shifts

In order to determine appropriate management actions, we will need to know if the dynamical behavior of the system we are currently observing is transient or asymptotic. This is particularly important if we need to anticipate a regime shift possibly resulting in a population collapse. The main difficulty here is that a regime shift associated with long transient dynamics may not contain a specific parameter of which variation would indicate a possible switch between regimes, as in the case of the 'classical' regime shift paradigm. Even if a transient-mediated regime shift would occur as a result of a change in a certain parameter (the habitat size, temperature, etc.), it is hard to predict eventual outcomes based only on the information about initial push, because transients can persist for many generations. Ecological time series are usually short and noisy and this makes it extremely complicated to determine whether the current stationary regime is actually a transient one.

There are several approaches to revealing transient dynamics. Most of them include a combination between mathematical modeling and analysis of empirical data; however, they vary according to the degree of modeling involved. The methods requiring less modeling are based on observation of the population dynamics, i.e. time series of species densities. Some of them are similar to those currently used in forecasting conventional regime shifts.

Simplest case for describing transients is where population densities show a clear change of dynamical pattern over time, for example in the case of the disappearance of periodic cycles of voles, lemmings and grouses in Europe [79]. Alternatively, it can be a slow but steady population decline, as in the extinction debt phenomena [145]. More challenging is the situation where the dynamics do not show a well pronounced trend. In this case, novel methods are needed to reveal possible presence of transient regimes. One recently developed promising method takes a Bayesian approach to nonlinear forecasting using Gaussian processes and only requires short time series [146]. This approach allows us to predict population dynamics for the next few steps. To uncover transients one can consider the population time series not only of the targeted species but also some other species with which the species interacts (competitors, predators or prey). The related species can show a more pronounced shift indicating the oncoming transient shift whereas the targeted species may remain fairly constant as was shown in some models [114]. Note that in the laboratory study of transient dynamics of *Tribolium* spp [29], the population size of adult beetles showed oscillation whereas those of larvae and pupae were constant during the transient stage.

A productive idea to uncover the ongoing transients in a complex ecological community is to compare its main characteristics with some universal relationship that is known for a typical healthy community at the stationary state or for the considered community in the past. An example can be anticipating the extinction debt caused by habitat fragmentation via comparing the current species richness related to the area with a similar pattern in the past [145]. While examinations of population densities may suggest stability, despite the changing habitat, other emergent prop-



System collapse (catastrophe)

Current Operating Point

Performing computations (e.g., bifurcation analysis) to determine if the system is in a transient state and to predict catastrophe before its occurrence

Using compressive sensing (sparse optimization) to accurately reconstruct system equations and parameters based on a small amount of measured data

Fig. 25. Schematic illustration of compressive sensing based framework for reconstructing system equations. The system can be in an asymptotically stable state or in a transient state but, at the current operating point, it exhibits no apparent shift in its dynamical behavior. Using short measured time series of all dynamical variables of the system, one can exploit compressive sensing to accurately reconstruct the system equations and parameters. One can then perform computational analyses to determine if the system is in a transient state and if a catastrophic collapse is imminent.

erties may signal transient behavior. For example, changes in the strength of the species-area relation can be a good indicator that currently the biodiversity is experiencing a transient regime [147].

A possible universal approach may consist in building a 'mechanistic' mathematical model based on first principles and fitted to empirical data. Exploring the model within realistic parameter ranges, one can use the current population sizes as initial conditions and conclude whether the ecosystem is currently experiencing transient dynamics or, alternatively, whether the influence of noise can destroy a deterministic attractor. This was done to predict the long transient in the extinction debt of butterflies in the UK [148]. On the other hand, construction of mechanistic models cannot be always possible (e.g. we do not know some key model parameters) and their predictions may not be accurate.

An alternative to constructing mechanistic models can be building a model entirely from the time series. In the past few years, a nonlinear systems identification framework was developed through exploiting compressive sensing [149–153] – a powerful sparse optimization approach. The basic principle of this approach is that the velocity fields of many natural and engineering systems are smooth functions that can be approximated by a finite series expansion. If the coefficients in the series representation can be accurately determined from measurements, the velocity field can be then reconstructed. Such a series would in general contain high order terms, so the total number of coefficients to be estimated can be quite large. However, if a large number of the coefficients are zero (or negligibly small), the vector constituting all the coefficients will be sparse, and the problem of sparse vector estimation can then be solved by the paradigm of compressive sensing [149–151] that reconstructs a sparse signal from limited observations. The idea of exploiting compressive sensing (or sparse optimization) for identifying equations of nonlinear dynamical systems was first introduced for predicting catastrophic bifurcation [154]. The approach was subsequently extended to reconstruct complex networks with discrete or continuous time nodal dynamics [155] and evolutionary game dynamics [156]. After constructing the model one can perform computational analysis to verify if our system is in a transient state. Fig. 25 illustrates the basic principle of the compressive sensing based reconstruction framework.

To understand the method, consider a nonlinear ecological system described by a system of ODEs

$$\frac{d\mathbf{x}}{dt} = \mathbf{F}(\mathbf{x}, \mathbf{p}), \tag{29}$$

where $\mathbf{x}(t)$ is the d-dimensional state vector, $\mathbf{F}$ is a vector of nonlinear model function, and $\mathbf{p}$ denotes a set of parameters. Assume that the system operates at a fixed set of parameter values: $\mathbf{p} = \mathbf{p}_0$, where the components of the state vector $\mathbf{x}(t)$ exhibit random but statistically stationary variations with time, i.e., there is no apparent shift in the dynamical behavior.

We would like to address the fundamental question of whether or not the system has reached a stable asymptotic state or is in a (possibly long) transient state.

For system (29), assuming that the current operating point is characterized by a fixed set of parameter values $\mathbf{p}_0$, in general we can expand the jth component of $\mathbf{F}(\mathbf{x}, \mathbf{p}_0)$ into a power series:

$$[\mathbf{F}(\mathbf{x}, \mathbf{p}_0)]_j = \sum_{l_1=0}^{n}\sum_{l_2=0}^{n} \cdots \sum_{l_m=0}^{n} (a_j)_{l_1,\cdots,l_m} \cdot x_1^{l_1} x_2^{l_2} \cdots x_m^{l_m}, \tag{30}$$

where x_k $(k = 1, \cdots, m)$ is the kth component of the dynamical variable, and the scalar coefficient of each product term $(a_j)_{l_1,\cdots,l_m} \in R$ is to be determined from measurements. Note that the terms in Eq. (30) are all possible products of different components with different powers, and there are $(1+n)^m$ terms in total.

To illustrate the basic principle of system equations reconstruction, we examine one dynamical variable. For example, for $m = 3$ (dynamical variables x, y, and z) and $n = 3$, we have the following explicit equation for the first dynamical variable:

$$[\mathbf{F}(\mathbf{x})]_1 \equiv (a_1)_{0,0,0} x^0 y^0 z^0 + (a_1)_{1,0,0} x^1 y^0 z^0 + \cdots + (a_1)_{3,3,3} x^3 y^3 z^3.$$

Denote the coefficients of $[\mathbf{F}(\mathbf{x})]_1$ by $\mathbf{a}_1 = [(a_1)_{0,0,0}, (a_1)_{1,0,0}, \cdots, (a_1)_{3,3,3}]^T$. Assuming that measurements of $\mathbf{x}(t)$ at a set of time $t_1, t_2, \ldots, t_w$ are available, we can write

$$\mathbf{g}(t) = \left[x(t)^0 y(t)^0 z(t)^0, x(t)^0 y(t)^0 z(t)^1, \cdots, x(t)^3 y(t)^3 z(t)^3\right]$$

such that $[\mathbf{F}(\mathbf{x}(t))]_1 = \mathbf{g}(t) \cdot \mathbf{a}_1$. From the expression of $[\mathbf{F}(\mathbf{x})]_1$, we can choose the measurement vector as

$$\mathbf{X} = [\dot{x}(t_1), \dot{x}(t_2), \cdots, \dot{x}(t_w)]^T,$$

which can be calculated from time series. We then obtain the standard compressive sensing equation of the form $\mathbf{X} = \mathcal{G} \cdot \mathbf{a}_1$:

$$\begin{pmatrix} \dot{x}(t_1) \\ \dot{x}(t_2) \\ \vdots \\ \dot{x}(t_w) \end{pmatrix} = \begin{pmatrix} \mathbf{g}(t_1) \\ \mathbf{g}(t_2) \\ \vdots \\ \mathbf{g}(t_w) \end{pmatrix} \begin{pmatrix} \mathbf{a}_1 \end{pmatrix}. \tag{31}$$

To ensure the restricted isometry property [157], we normalize $\mathcal{G}$ by dividing elements in each column by the L_2 norm of that column: $(\mathcal{G}')_{ij} = (\mathcal{G})_{ij}/L_2(j)$ with $L_2(j) = \sqrt{\sum_{i=1}^{M}[(\mathcal{G})_{ij}]^2}$, so that $\mathbf{X} = \mathcal{G}' \cdot \mathbf{a}_1'$. After the normalization, $\mathbf{a}_1' = \mathbf{a}_1 \cdot L_2$ can be determined via a standard compressive-sensing algorithm [157]. As a result, the coefficients $\mathbf{a}_1$ are given by $\mathbf{a}_1'/L_2$. To determine the set of power-series coefficients corresponding to a different dynamical variable, say y, we simply replace the measurement vector by $\mathbf{X} = [\dot{y}(t_1), \dot{y}(t_2), \cdots, \dot{y}(t_w)]^T$ and use the same matrix $\mathcal{G}$. This way all coefficients $\mathbf{a}_1$, $\mathbf{a}_2$, and $\mathbf{a}_3$ in the three dimensions can be estimated. In Ref. [154], a number of classic chaotic systems were used to demonstrate the principle of compressive sensing based reconstruction of system equations from sparse measurements.

8. Discussion

Robust and timely forecast of any significant change in ecosystem's state, function and properties is required in order to ensure efficient ecosystem management, especially in the face of great current challenges such as global warming, habitat fragmentation, biological invasions, etc. Reliable forecasts require a good understanding of patterns of ecosystem dynamics through the identification of the factors and mechanisms responsible for the change. Statistical analysis of field data routinely used in ecology may not always be sufficient, especially when an ecosystem undergoes a regime shift resulting in a qualitative change in the system state and/or dynamics. Mathematical modeling has long been used as a powerful supplement and sometimes even alternative to statistical ecology. In particular, mathematical models of population dynamics have greatly facilitated the progress made in ecology, as well as in the life sciences more broadly, over the last few decades.

The standard use of mathematical models, however, usually focuses on their large-time asymptotical behavior, that is, in the context of the dynamical systems theory, on the model's attractors. However, there have been growing understanding and increasing amount of evidence that often the time required for the system to converge to the attractor is very long [15–21]. It means that any inferences made about the ecosystem dynamics based only on the geometry of the attracting invariant sets can be misleading and the corresponding management decisions are likely to be inefficient or even irrelevant. Transient dynamics of mathematical models, especially long transients are arguably more relevant to ecosystem dynamics than the asymptotical properties that in real-world systems may be never reached.

Interestingly, although long transients have been a topic of considerable interest in physics, there has been surprisingly little theoretical work done about this in the context of ecology. In order to bridge the gap, in this paper we have provided a rather comprehensive review along with necessary 'close-to-rigorous' mathematical analysis of ecologically relevant models that exhibit long-term transient dynamics. Several baseline mechanisms resulting in long transients have been identified and analyzed, such as ghost attractors, crawl-bys (saddles), slow-fast systems, noised-induced transients, transients caused by wave propagation, spatial chaotic transients and transients in systems with delay. The dependence of the transient's lifetime on the controlling parameters as well as their properties more generally have been revealed and discussed; see Tables 1 and 2 for a brief summary.

Note that one general mathematical property of the nonspatial models exhibiting long transients is the existence of a small parameter. The smaller the parameter is, the longer the transient lasts, tending to infinity (according to a given scaling law) when the parameter tends to zero. In slow-fast systems, this is obviously a defining property (see Section 3.3). For transients associated with saddles, the small parameter is the largest eigenvalue; see Eq. (4). For ghosts attractors, it is less obvious. However, we recall that, for the transients to be caused by ghost attractors, the system must be just beyond the tipping point. Let p be the controlling parameter and p_c is its critical value corresponding to the bifurcation. Then "just beyond" means that $\tilde{p} = |p - p_c|/p_c$ is small. In a general case, the controlling parameter p can be a combination of the original parameters and as such might not have a clear biological meaning. Therefore, the fact that $\tilde{p}$ is small does not necessarily mean that any of the parameters with immediate biological meaning (e.g. growth rates, mortality rates, etc.) is small. With spatial models, the situation is essentially the same except for the dependence on the system size, which is exact opposite: the transient's lifetime grows unboundedly when the system size tends to infinity.

Our study reveals the connection between long transients and tipping points. For a transient to emerge, there must be a factor that pushes the system out of its stable equilibrium (or, more generally, out of its stable dynamics). Apparently, such a push can be a result of perturbation applied to the state variables, e.g. it can be associated with noise. Alternatively, it can result from a structural perturbation: a bifurcation that eliminates the steady state altogether (see Section 3.2). Once the equilibrium disappears, the system starts converging to another attractor. The important difference between the 'conventional' and the long-term transient scenarios is that the required initial perturbation may have happened long time ago. An observer would then need to deal with the long-term transient dynamics but without knowing the event that had triggered it. Besides, the question as to what is the specific change that can break the stability of the ecosystem is not always clear; hence it can easily remain unidentified. Therefore, the danger of the transient-related regime shift is that, over the time of observation, the system's parameters would apparently remain unchanged. Moreover, if the system is just beyond the tipping point, the rate of changes in its state is very low (see Fig. 26). Altogether, it may give a false impression that the system remains in a stable steady state (or in a sustainable dynamical regime).

However, the existence of long transients also opens a possibility for a regime shift to occur without any preceding structural perturbation at all. This happens in case of *recurrent* long transients, e.g. see Figs. 1b, 4, 5, 11 and 13. In this case, the long-term regimes are not large-time limits of the system's dynamics but stages in a periodic or quasi-periodic dynamics occurring on a much longer time scale.

Understanding of the relation between tipping points and long transients has immediate implications for ecosystems management. As an illuminating example, consider the paradigmatic case where the unique positive stable steady state disappears as a result of a saddle-node bifurcation and the only remaining attractor is the extinction state; see Fig. 26. Once the system is beyond the tipping point, the population starts declining. A straightforward management response might try to counteract this tendency by increasing the population numbers (e.g. by means of artificial breeding), see Arrow 1 in Fig. 26. However, this response cannot bring the system back to the safe state: at this parameter value the stable steady state does not exist. Therefore, this approach is unlikely to be efficient unless the desired ecosystem state is the transient state; in the latter case, the approach consisting of periodical interventions (which, in mathematical

Table 1
Overview of long transients in different nonspatial models of population dynamics and their scaling behavior. Index “c” marks the critical (bifurcation) value of the parameter, NAIS stands for a non-attracting invariant set.

System (model)	Discrete or continuous	Type of transient	Controlling parameter(s)	Lifetime’s scaling law	Mechanism (NAIS)
General multi-species, Eqs. (1)	Continuous	Regular (quasi-steady state)	Largest eigenvalue, λ_1	$\tau \propto \frac{1}{\lambda_1}$	Crawl-by (saddle), non-recurrent
Prey-predator, Eqs. (7)–(8)	Continuous	Regular (quasi-steady states)	Prey’s carrying capacity	As above, for each of the saddles	Crawl-bys (limit cycle, saddles), recurrent
Three-species cyclic competition [46,45], ODEs	Continuous	Regular (quasi-steady states)	Parameter combination, π	$\tau \propto \pi^T, \pi > 1, T = 1, 2, \ldots$	Crawl-bys (heteroclinic connection, saddles), recurrent
Three-species food chain [71,61], ODEs	Continuous	Chaotic	Resource’s carrying capacity, K	$\tau \propto (K - K_c)^{-\gamma}, \gamma > 0$	Chaotic saddle, non-recurrent
Plankton-oxygen, Eqs. (11)–(12), see also the appendix	Continuous	Regular (quasi-steady state)	Oxygen production rate, A	$\tau \propto (A - A_c)^{-\gamma}, \gamma \geq 0$	Ghost, non-recurrent
Generic dynamical system [77,78]	Discrete	Chaotic	Parameter combination, p	$\tau \propto \exp\left[a(p - p_c)^{-\gamma}\right], \gamma > 1$	Chaotic ghost, non-recurrent
Slow-fast system, Eqs. (14)	Continuous	Regular	Ratio of time-scales, ϵ	$\tau \propto \epsilon^{-1}, \epsilon \ll 1$	Separation of time-scales, recurrent or non-recurrent
Slow-fast system with control [96]	Discrete	Intermittent regular and/or chaotic oscillations	Control parameter, $\epsilon \ll 1$	No data	Separation of time-scales, recurrent or non-recurrent
Single-species map with weak (undercritical) noise [109]	Discrete	Chaotic	Noise strength, ϵ	$\tau \propto \exp[K_0 \exp(K_1 \varepsilon^{-\gamma})], \epsilon < \epsilon_c$	Interaction of noise with chaotic attractor, non-recurrent
Single-species map with strong (supercritical) noise [109]	Discrete	Chaotic	Noise strength, ϵ	$\tau \propto \exp(C\varepsilon^{-\gamma}), \epsilon > \epsilon_c$	Interaction of noise with chaotic attractor, non-recurrent

Table 2
Overview of long transients in spatial models of population dynamics, RD stands for reaction-diffusion. .

System (model)	Discrete or continuous	Initial conditions	Type of transient	Controlling parameter (s)	Transient's scaling law	Mechanism
Single-species, scalar RD equation	Space-time-continuous	Compact	Regular (traveling population front, Fig. 16)	Domain size L, front's speed c	$\tau \propto \frac{L}{c}$	Heteroclinic connection
Prey-predator, RD system (21) [118]	Space-time-continuous	Compact	Regular (periodic wavetrain, Fig. 17a)	Parameter combination, p	$W \propto p^{-\gamma}$, $\gamma > 0$, W is wavetrain's length	Heteroclinic connection
Prey-predator, RD system (21) [117,115]	Space-time-continuous	Compact	Regular (unstable plateau – dynamical stabilization, Fig. 17b)	Parameter combination, p	$W \propto p^{-\gamma}$, $\gamma > 0$, W is plateau length	Heteroclinic connection
Prey-predator, RD system (21) [122]	Space-time-continuous	Compact	Spatiotemporal chaos, Fig. 19	Parameter combination, p	No data	Ghost attractor
Prey-predator, RD system (21) [116]	Space-time-continuous	Distributed	Spatiotemporal chaos ('wave of chaos', Fig. 20)	Domain size L, eigenvalue at coexistence state λ	$\tau \propto L(\mathrm{Re}\,\lambda)^{-1/2}$	Unknown
Three competing species, RD system [120], 1D space	Space-time-continuous	Compact	Regular (unstable plateau – dynamical stabilization)	Parameter combination	No data	Heteroclinic connection
Three competing species, RD system [121], 2D space	Space-time-continuous	Distributed	Regular spatial patterns, Fig. 18	Parameter combination	No data	Unknown
Plankton-oxygen, three species RD system [63,64]	Space-time-continuous	Distributed	Spatiotemporal chaos, Fig. 21	Oxygen production rate	No data	Chaotic ghost
General RD system [124]	Space-time-continuous	Distributed	Spatiotemporal chaos	Domain size L	$\tau \propto L^{\gamma_1}$ or $\tau \propto \exp\left(aL^{\gamma_2}\right)$, $\gamma_{1,2} > 0$	Chaotic saddle
Single-species with delay, RD equation with delay [136]	Space-time-continuous	Compact	Regular (unstable plateau), Fig. 24	Time lag	No data	Heteroclinic connection
Single-species with stage structure, Eq. (24) [125]	Space-continuous, discrete-time	Distributed	Regular or chaotic	Growth rate	No data	Chaotic saddle
1D array of N coupled maps, Eq. (27) [72]	Space-time-discrete	Distributed	Spatiotemporal chaos	System's size N, coupling strength μ	$\tau \propto N^{\gamma_1}$ for $\mu < \mu_c$, $\tau \propto \exp\left(aN^{\gamma_2}\right)$ for $\mu > \mu_c$, $\gamma_{1,2} > 0$	Chaotic saddle

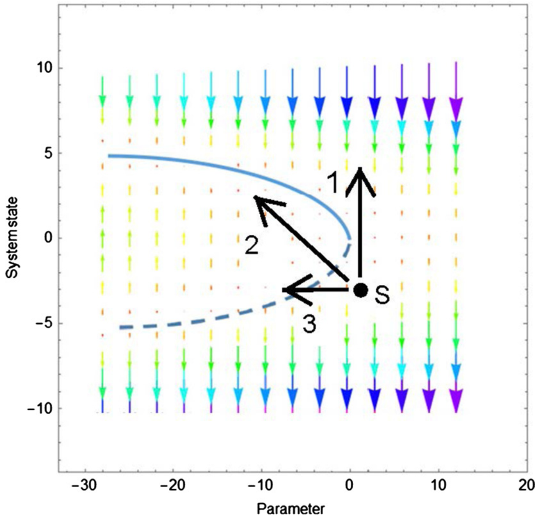


Fig. 26. Sketch of different ecosystem management strategies in case the ecosystem experiences a long term transient dynamics beyond the tipping point. Black ball *S* shows the hypothetical state of a given population community experiencing a 'free fall' to extinction after the system experienced a bifurcation that eliminated the stable steady state. Different arrows correspond to different management strategies: arrow 1 for the strategy focusing on restoring the population numbers without changing the environment, arrow 2 for the strategy to restore the population numbers along with changing environment, arrow 3 for the strategy to only change the environment without restoring the population numbers. From [21], adapted.

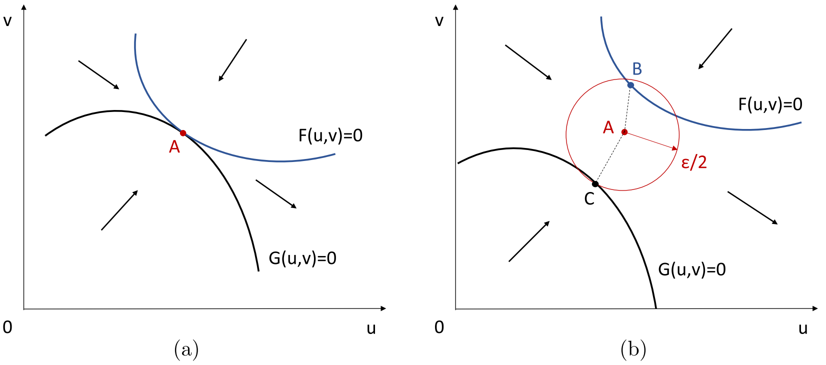
terms, can be associated with the flow-kick dynamics [28,158]) must be a part of a long-term management strategy. An alternative strategy aiming to restore the environment to its before-bifurcation state without increasing the population numbers (see Arrow 3) might not be sufficient because of the threshold effect of the unstable steady state (the dashed curve in Fig. 26): unless the environmental restoration is substantial enough, the system would remain in the attraction basin of the extinction state. Therefore, one can expect that a more efficient strategy should be the one that combines restoration with measures to increase the population numbers (cf. Arrow 2).

A major issue arises with regard to reliable ways to reveal and forecast long transients in natural systems. One considerable challenge is development of the mathematical and computational framework to distinguish transients from the asymptotical dynamics. Although some progress has recently been made (cf. Section 7), this area of research is still in its mathematical infancy. The situation is different compared to the well-established theory of early warming signals for tipping points [14,13]. We believe that the classification and analysis of possible transient regimes, scenarios and mechanisms provided in this paper will facilitate the development of relevant mathematical methods and tools for efficient ecological forecasting.

Ecologists have long been aware, often intuitively, about the importance of transient dynamics. It has been increasingly recognized that, much of their time, ecological systems are far away from stable states or even from stable dynamical regimes [18,19,30,31,36,76,82,125]. A systematic consideration of this notion has been largely lacking though. In this paper, we have endeavored to develop a consistent theoretical framework to deal with transients, especially long transients. Such framework can be useful for better understanding of many old and new problems such as, for instance, the extinction debt [16,145] and challenges associated with the global climate change. Application of the framework to specific ecological cases and systems will require a considerable additional work. Such work should become a focus of future research.

Acknowledgements

This paper has emerged as a result of the Working Group "Long Living Transients as a Bugbear of Ecological Forecasting: Concepts, Models and Data" funded by NIMBioS (The National Institute for Mathematical and Biological Synthesis, Knoxville TN) in 2017-19. Supportive attitude of NIMBioS directors Lou Gross and Sergey Gavrilets is greatly appreciated. Insightful comments of two anonymous reviewers helped to improve the manuscript. This work was presented and thoroughly discussed at the Banff workshop "New Mathematical Methods for Complex Sys-



(a) (b)

Fig. 27. Sketch of the phase plane structure corresponding to the emergence of a ghost attractor. (a) Relative position of the isoclines for the critical value p_c of the parameter where two positive steady states, a stable node and a saddle, merge to create a single steady state A. (b) Relative position of the isoclines for $p > p_c$ where distance ϵ is small if $\delta = p - p_c$ is sufficiently small. Arrows indicate the generic direction of the phase flow.

tems in Ecology" (July 28 to August 2, 2019). Helpful comments from Chris Cosner, Christian Kuehn and Sebastian Schreiber are particularly appreciated. Some computational results were obtained in the framework of the state assignment of Russia (theme No. 0149-2019-0004) and partially supported by RFBR through Project766 No. 17-05-00799 (to A.M.). The publication has been prepared with the support of the "RUDN University Program 5-100" (to S.P.).

Appendix A. Scaling law for a ghost attractor

Consider a general two-species system described by the following equations:

$$\dot{u}(t) = F(u, v; p), \qquad \dot{v}(t) = G(u, v; p), \tag{32}$$

where the dot denotes the derivative with respect to time and p is a certain controlling parameter. We assume that the dependence of F and G on p is smooth, so that the dependence of the system properties (e.g. the position of the isoclines in the phase plane) depends on p continuously.

We focus on the case where functions F and G are such that the isoclines of the system have a concave-convex shape hence allowing for the existence of two steady states (e.g. see Fig. 7a in the main text) in a certain range of parameter p, say for $p < p_c$. With an increase in p, the isoclines moves away from each other, so that the steady states moves towards each other, merge for $p = p_c$ (cf. Fig. 27a) and disappear, usually in a saddle-node bifurcation. For $p > p_c$, there are no steady states as the isoclines do not intersect any more. We mention here that this type of a population model's response to a change in a relevant parameter is in fact rather general; examples are given by the nonlinear competition model [15], the oxygen-phytoplankton model [63] (see also Section 3.2) and Scheffer's plankton-fish model [159,160].

At the bifurcation value $p = p_c$, the isoclines have a single joint point, say A (Fig. 27a). Let the corresponding points at F-isocline and G-isocline be B and C, respectively. We now mark the position of these points at the corresponding curves (e.g. by choosing a relevant parametrization of the curves) and trace the change in their position in the phase plane as a result of an increase in p. When parameter p increases from its bifurcation value, points B and C moves away from each other (Fig. 27b). However, since the dependence on p is assumed to be continuous, for the values of p just slightly larger than p_c, the distance between points B and C (and hence the distance between the isolines) is small. This can be rephrased in a more rigorous way. Let d_{AB}, d_{AC} and d_{BC} be the distances between the corresponding points and $\bar{d} = \max\{d_{AB}, d_{AC}, d_{BC}\}$. Then for any $\epsilon > 0$ (arbitrarily small), there exist δ such that, for any $p \in (p_c, p_c + \delta)$, $\bar{d} < \epsilon$ (Fig. 27b).

We now consider A as a certain 'reference point' and estimate the time that the system spends in the vicinity of A. We therefore need to estimate the value of $\dot{u}$ and $\dot{v}$ in the vicinity of A. For this purpose, we consider system (32) where the right-hand sides are transformed using the Taylor formula for a function of two variables:

$$\dot{u}(t) = F(u_B, v_B; p) + \big((\nabla F)_B \cdot \mathbf{e}_{BA}\big) d_{AB} + o(d_{AB}), \tag{33}$$

$$\dot{v}(t) = G(u_C, v_C; p) + \big((\nabla G)_C \cdot \mathbf{e}_{CA}\big) d_{AC} + o(d_{AC}). \tag{34}$$

Here $\mathbf{e}_{BA}$ is the unit vector in the direction from B to A, $\mathbf{e}_{CA}$ is the unit vector in the direction from C to A, and

$$(\nabla F) = \left(\frac{\partial F}{\partial u}\right)\mathbf{e}_u + \left(\frac{\partial F}{\partial v}\right)\mathbf{e}_v, \quad (\nabla G) = \left(\frac{\partial G}{\partial u}\right)\mathbf{e}_u + \left(\frac{\partial G}{\partial v}\right)\mathbf{e}_v, \tag{35}$$

where $\mathbf{e}_u$ and $\mathbf{e}_v$ are the unit vectors of axes u and v, respectively.

Taking into account that $F(u_B, v_B; p) = 0$ and $G(u_C, v_C; p) = 0$, because points B and C belongs to the u-isocline and v-isocline, respectively, from (33)–(34) we obtain:

$$|\dot{u}| = \left|\big((\nabla F)_B \cdot \mathbf{e}_{BA}\big)d_{AB} + o(d_{AB})\right| \ \le\ \left|\big((\nabla F)_B \cdot \mathbf{e}_{BA}\big)d_{AB}\right| + |o(d_{AB})| \\ \le \left|\big((\nabla F)_B\right|\epsilon + |o(\epsilon)|, \tag{36}$$

$$|\dot{v}| = \left|\big((\nabla G)_C \cdot \mathbf{e}_{CA}\big)d_{AC} + o(d_{AC})\right| \ \le\ \left|\big((\nabla G)_C \cdot \mathbf{e}_{CA}\big)d_{AC}\right| + |o(d_{AC})| \\ \le \left|\big((\nabla G)_C\right|\epsilon + |o(\epsilon)|, \tag{37}$$

where we also took into account that $\max\{d_{AB}, d_{AC}, d_{BC}\} < \epsilon$.

Obviously,

$$T_\epsilon^A \sim \frac{\chi_\epsilon}{S}, \tag{38}$$

where T_ϵ^A is the time that the system spends in the close vicinity of point A, χ_ϵ is the size of the vicinity in the tangential direction, and S is the speed of the system's movement along its trajectory in the phase plane. Since $S = |\mathbf{S}|$ where $\mathbf{S} = (\dot{u}, \dot{v})$ is the corresponding velocity, we obtain that

$$S = \sqrt{\dot{u}^2 + \dot{v}^2}. \tag{39}$$

From (39) and (36)–(37), in the first order of ϵ, we obtain:

$$S = \epsilon\sqrt{\big(\nabla F\big)_B^2 + \big(\nabla G\big)_C^2} \ \sim\ \epsilon. \tag{40}$$

The choice of χ_ϵ depends on the definition of the closeness to point A. Perhaps the most straightforward would be the spherical vicinity of radius ϵ (cf. Fig. 27b). However, this definition is not constructive as it misses the fact that, due to the assumed smoothness of the curves, the size of the vicinity where the isoclines lie close to each other (and hence the dynamics are very slow) in the tangential direction is actually significantly larger than in the transversal direction. Having taken the effects of the isocline's curvature into account, it is readily seen that

$$\chi_\epsilon \sim \epsilon^\sigma, \tag{41}$$

where $\sigma = 0.5$ in a standard, non-generated case where the isoclines are approximated by the second order algebraic curves; in a more general case $0 < \sigma < 1$.

From (38), (40) and (41), we therefore obtain:

$$T_\epsilon^A \sim \epsilon^{-(1-\sigma)}\ . \tag{42}$$

In case $\sigma = 0.5$, Eq. (42) coincides with the result obtained by Strogatz [39] for the quadratic nonlinearity; see p. 99 in [39].

Thus, when the distance ϵ between the isoclines tends to zero, the time that the system spends in the narrow channel tends to infinity as an inverse power law of the distance. Note that, generally speaking, ϵ is not the controlling parameter. However, due to the continuous dependence on parameter p, ϵ must be a monotonously decreasing function of the difference $(p - p_c)$ tending to zero for $(p - p_c) \to 0$. Therefore, the lifetime $\tau = T_\epsilon^A$ of the transient caused by the ghost attractor tends to infinity for $p \to p_c$; however, the precise form of the scaling law can vary depending on the choice of the controlling parameter.

References

[1] Dietze MC. Prediction in ecology: a first-principles framework. Ecol Appl 2017;27(7):2048–60.
[2] May RM. Simple mathematical models with very complicated dynamics. Nature 1976;261(5560):459–67.
[3] Hastings A, Hom CL, Ellner S, Turchin P, Godfray HCJ. Chaos in ecology: is mother nature a strange attractor? Annu Rev Ecol Evol Syst 1993;24(1):1–33.
[4] Cushing JM, Costantino RF, Dennis B, Desharnais R, Henson SM. Chaos in ecology: experimental nonlinear dynamics. Elsevier; 2002.
[5] Coulson T, Rohani P, Pascual M. Skeletons, noise and population growth: the end of an old debate? Trends Ecol Evol 2004;19:359–64.
[6] Greenman JV, Benton TG. The amplification of environmental noise in population models: causes and consequences. Am Nat 2003;161(2):225–39.
[7] Abbott KC, Nolting BC. Alternative (un)stable states in a stochastic predator–prey model. Ecol Complex 2017;32:181–95.
[8] Fussmann GF, Blasius B. Community response to enrichment is highly sensitive to model structure. Biol Lett 2005;1:9–12.
[9] Cordoleani F, Nerini D, Gauduchon M, Morozov A, Poggiale JC. Structural sensitivity of biological models revisited. J Theor Biol 2011;283:82–91.
[10] Adamson MW, Morozov AYu. When can we trust our model predictions? Unearthing structural sensitivity in biological systems. Proc R Soc A 2013;469:20120500.
[11] Scheffer M, Straile D, van Nes EH, Hosper H. Climatic warming causes regime shifts in lake food webs. Limnol Oceanogr 2001;46(7):1780–3.
[12] Carpenter SR, Cole JJ, Pace ML, et al. Early warnings of regime shifts: a whole-ecosystem experiment. Science 2011;332(6033):1079–82.
[13] Boettiger C, Hastings A. Quantifying limits to detection of early warning for critical transitions. J R Soc Interface 2012;9:2527–39.
[14] Dakos V, Carpenter SR, Brock WA, et al. Early warning signals of critical transitions: methods for time series. PLoS ONE 2012;7:e41010.
[15] Hastings A, Abbott KC, Cuddington K, et al. Transient phenomena in ecology. Science 2018;361:eaat6412.
[16] Tilman D, May RM, Lehman CL, Nowak MA. Habitat destruction and the extinction debt. Nature 1994;371(6492):65–6.
[17] Stott I, Hodgson DJ, Townley S. Beyond sensitivity: nonlinear perturbation analysis of transient dynamics. Methods Ecol Evol 2012;3(4):673–84.
[18] Hastings A. Transient dynamics and persistence of ecological systems. Ecol Lett 2001;4:215–20.
[19] Hastings A. Transients: the key to long-term ecological understanding? Trends Ecol Evol 2004;19:39–45.
[20] Wilson RS, Hardisty DJ, Epanchin-Niell RS, et al. A typology of time-scale mismatches and behavioral interventions to diagnose and solve conservation problems. Conserv Biol 2015;30:42–9.
[21] Hastings A. Timescales and the management of ecological systems. Proc Natl Acad Sci USA 2016;113:14568–73.
[22] Izhikevich EM. Dynamical systems in neuroscience: the geometry of excitability and bursting. Computational neuroscience; 2006.
[23] Rabinovich M, Huerta R, Laurent G. Transient dynamics for neural processing. Science 2008:48–50.
[24] Tufcea DE, François P. Critical timing without a timer for embryonic development. Biophys J 2015;109(8):1724–34.
[25] Lai Y-C, Winslow RL. Geometric properties of the chaotic saddle responsible for supertransients in spatiotemporal chaotic systems. Phys Rev Lett 1995;74(26):5208–11.
[26] Lorenz H-W, Nusse HE. Chaotic attractors, chaotic saddles, and fractal basin boundaries: Goodwin's nonlinear accelerator model reconsidered. Chaos Solitons Fractals 2002;13(5):957–65.
[27] Medeiros ES, Caldas IL, Baptista MS, Feudel U. Trapping phenomenon attenuates the consequences of tipping points for limit cycles. Sci Rep 2017;7:42351.
[28] Meyer K, Hoyer-Leitzel A, Iams S, et al. Quantifying resilience to recurrent ecosystem disturbances using flow-kick dynamics. Nat Sustain 2018;1:671–8.
[29] Cushing JM, Dennis B, Desharnais RA, Costantino RF. Moving towards unstable equilibrium: saddle nodes in population systems. J Anim Ecol 1998;67:298–306.
[30] Van Geest GJ, Coops H, Scheffer M, van Nes EH. Long transients near the ghost of a stable state in eutrophic shallow lakes with fluctuating water levels. Ecosystems 2005;10:36–46.
[31] Watt AS. Pattern and process in the plant community. J Ecol 1947;35(1/2):1–22.
[32] Schröder A, Persson L, De Roos AM. Direct experimental evidence for alternative stable states: a review. Oikos 2005;110(1):3–19.
[33] Hutchinson GE. The paradox of the plankton. Am Nat 1961;95:137–45.
[34] Connell JH. Diversity in tropical rain forests and coral reefs. Science 1978;199:1302–10.
[35] Botkin DB. Discordant harmonies: a new ecology for the twenty-first century. New York: Oxford University Press; 1990.
[36] Rohde K. Nonequilibrium ecology. Cambridge UK: Cambridge University Press; 2006.
[37] Morozov A, Banerjee M, Petrovskii S. Long-term transients and complex dynamics of a stage-structured population with time delay and the Allee effect. J Theor Biol 2016;396:116–24.
[38] Lorenz EN. Deterministic nonperiodic flow. J Atmos Sci 1963;20:130–41.
[39] Strogatz SH. Nonlinear dynamics and chaos. Cambridge MA: Perseus Books Publishing; 1994.
[40] Sharma Y, Abbott KC, Dutta PS, Gupta AK. Stochasticity and bistability in insect outbreak dynamics. Theor Ecol 2015;8:163–74.
[41] Allen LSJ. An introduction to mathematical biology. Upper Saddle River: Pearson Prentice Hall; 2007.
[42] Rosenzweig ML, MacArthur RH. Graphical representation and stability conditions of predator-prey interactions. Am Nat 1963;97:209–23.
[43] Rosenzweig ML. Paradox of enrichment: destabilization of exploitation ecosystem in ecological time. Science 1971;171:385–7.
[44] Jager CG, Diehl S, Matauschek C, Klausmeier CA, Stibor H. Transient dynamics of pelagic producer grazer systems in a gradient of nutrients and mixing depths. Ecology 2008;89:1272–86.
[45] May RM, Leonard WJ. Nonlinear aspects of competition between three species. SIAM J Appl Math 1975;29(2):243–53.

[46] Hofbauer J, Sigmund K. Evolutionary games and population dynamics. Cambridge University Press; 1998.
[47] Guckenheimer J, Holmes P. Structurally stable heteroclinic cycles. Mathematical proceedings of the Cambridge Philosophical Society, vol. 103. Cambridge University Press; 1988. p. 189–92.
[48] Buono P-L, Golubitsky M, Palacios A. Heteroclinic cycles in rings of coupled cells. Physica D 2000;143(1–4):74–108.
[49] Krupa M. Robust heteroclinic cycles. J Nonlinear Sci 1997;7(2):129–76.
[50] Sinervo B, Lively CM. The rock–paper–scissors game and the evolution of alternative male strategies. Nature 1996;380(6571):240–3.
[51] Kirkup BC, Riley MA. Antibiotic-mediated antagonism leads to a bacterial game of rock–paper–scissors in vivo. Nature 2004;428(6981):412–4.
[52] Paquin CE, Adams J. Relative fitness can decrease in evolving asexual populations of s. cerevisiae. Nature 1983;306(5941):368–71.
[53] Ashwin P, Timme M. Nonlinear dynamics: when instability makes sense. Nature 2005;436(7047):36–7.
[54] Cushing JM, Costantino RF, Dennis B, Desharnais RA, Henson SM. Nonlinear population dynamics: models, experiments and data. J Theor Biol 1998;194:1–9.
[55] Kuehn C, Zschaler G, Gross T. Early warning signs for saddle-escape transitions in complex networks. Sci Rep 2015;5:13190.
[56] Laurent G. Olfactory network dynamics and the coding of multidimensional signals. Nat Rev Neurosci 2002;3(11):884–95.
[57] Lai Y-C, Grebogi C, Yorke JA, Venkataramani S. Riddling bifurcation in chaotic dynamical systems. Phys Rev Lett 1996;77:55–8.
[58] Grebogi C, Ott E, Yorke JA. Crises, sudden changes in chaotic attractors and chaotic transients. Physica D 1983;7:181–200.
[59] Grebogi C, Ott E, Romeiras F, Yorke J. Critical exponents for crisis-induced intermittency. Phys Rev A 1987;36:5365–80.
[60] Sommerer JC, Ditto W, Grebogi C, Ott E, Spano M. Experimental confirmation of the theory for critical exponents of crises. Phys Lett A 1991;153:105–9.
[61] McCann K, Yodzis P. Nonlinear dynamics and population disappearances. Am Nat 1994;144:873–9.
[62] Duarte J, Januário C, Martins N, Sardanyés J. On chaos, transient chaos and ghosts in single population models with Allee effects. Nonlinear Anal, Real World Appl 2012;13(4):1647–61.
[63] Sekerci Y, Petrovskii S. Mathematical modelling of plankton-oxygen dynamics under the climate change. Bull Math Biol 2015;77:2325–53.
[64] Petrovskii S, Sekerci Y, Venturino E. Regime shifts and ecological catastrophes in a model of plankton-oxygen dynamics under the climate change. J Theor Biol 2017;424:91–109.
[65] Sekerci Y, Petrovskii S. Global warming can lead to depletion of oxygen by disrupting phytoplankton photosynthesis: a mathematical modelling approach. Geosciences 2018;8:201.
[66] Tyukin I. Adaptation in dynamical systems. Cambridge UK: Cambridge University Press; 2011.
[67] Gorban AN, Cheresiz VM. Slow relaxations of dynamical systems and bifurcations of ω-limit sets. Dokl Akad Nauk SSSR 1981;261(5):1050–4.
[68] Gorban AN, Karlin IV, Zinovyev AY. Constructive methods of invariant manifolds for kinetic problems. Phys Rep 2004;396:197–403.
[69] Gorban AN. Singularities of transition processes in dynamical systems: qualitative theory of critical delays. Electr J Diff Equ, Monograph 2004;05.
[70] Pomeau Y, Manneville P. Intermittent transition to turbulence in dissipative dynamical systems. Commun Math Phys 1980;74(2):189–97.
[71] Hastings A, Powell T. Chaos in a three-species food chain. Ecology 1991;72:896–903.
[72] Lai Y-C, Tél T. Transient chaos - complex dynamics on finite-time scales. New York: Springer; 2011.
[73] Ott E. Chaos in dynamical systems. 2nd edition. Cambridge, UK: Cambridge University Press; 2002.
[74] Grebogi C, McDonald SW, Ott E, Yorke JA. Exterior dimension of fat fractals. Phys Lett A 1985;110:1–4.
[75] Grebogi C, Ott E, Yorke JA. Comment on "sensitive dependence on parameters in nonlinear dynamics" and on "fat fractals on the energy surface". Phys Rev Lett Jan 1986;56:266.
[76] Schreiber SJ. Allee effects, extinctions, and chaotic transients in simple population models. Theor Popul Biol 2003;64(2):201–9.
[77] Grebogi C, Ott E, Yorke JA. Fractal basin boundaries, long-lived chaotic transients, and unstable-unstable pair bifurcation. Phys Rev Lett 1983;50:935–8.
[78] Grebogi C, Ott E, Yorke JA. Super persistent chaotic transients. Ergod Theory Dyn Syst 1985;5:341–72.
[79] Ims R, Henden JA, Killengreen ST. Collapsing population cycles. Trends Ecol Evol 2008;23:79–86.
[80] Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 2009;90:1478–84.
[81] Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR. Long-term region-wide declines in Caribbean corals. Science 2003;301:958–60.
[82] Frank KT, Petrie B, Fisher JAD, Leggett WC. Transient dynamics of an altered large marine ecosystem. Nature 2011;477:86–9.
[83] Harding JS, Benfield EF, Bolstad PV, Helfman GS, Jones EBD. Stream biodiversity: the ghost of land use past. Proc Natl Acad Sci USA 1998;95:14843–7.
[84] Deco G, Senden M, Jirsa V. How anatomy shapes dynamics: a semi-analytical study of the brain at rest by a simple spin model. Front Comput Neurosci 2012;6:68.
[85] Rinaldi S, Muratori S. Slow-fast limit cycles in predator-prey models. Ecol Model 1992;61:287–308.
[86] De Feo O, Rinaldi S. Singular homoclinic bifurcations in tritrophic food chains. Math Biosci 1998;148:7–20.
[87] Kooi BW, Poggiale JC. Modelling, singular perturbation and bifurcation analyses of bitrophic food chains. Math Biosci 2018;301:93–110.
[88] Ludwig D, Jones DD, Holling CS. Qualitative analysis of insect outbreak systems: the spruce budworm and forest. J Anim Ecol 1978:315–32.
[89] Timms RM, Moss B. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. Limnol Oceanogr 1984;29:472–86.
[90] Franks PJS. Phytoplankton blooms in a fluctuating environment: the roles of plankton response time scales and grazing. J Plankton Res 2001;23:1433–41.
[91] Morozov A, Arashkevich E, Nikishina A, Solovyev K. Nutrient-rich plankton communities stabilized via predator-prey interactions: revisiting the role of vertical heterogeneity. Math Med Biol 2011;28(2):185–215.

[92] Hairer E, Wanner G. Solving ordinary differential equations II: stiff and differential-algebraic problems. 2nd edition. Berlin: Springer-Verlag; 1996.

[93] Burden RL, Faires JD. Numerical analysis. 9th edition. Boston: Brooks/Cole; 2011.

[94] Kuehn C. Multiple time scale dynamics. Springer; 2015.

[95] Rinaldi S, Scheffer M. Geometric analysis of ecological models with slow and fast processes. Ecosystems 2000;3:507–21.

[96] Singh BK, Parham PE, Hu C-K. Structural perturbations to population skeletons: transient dynamics, coexistence of attractors and the rarity of chaos. PLoS ONE 2011;6(9):e24200.

[97] Krauskopf J, Desroches B, Guckenheimer M, et al. Mixed-mode oscillations with multiple time scales. SIAM Rev 2012;54(2):211–88.

[98] Kaneko K, Tsuda I. Chaotic itinerancy. Chaos 2003;13(3):926–36.

[99] Valenti D, Fiasconaro A, Spagnolo B. Stochastic resonance and noise delayed extinction in a model of two competing species. Physica A 2004;331:477–86.

[100] Higgins K, Hastings A, Sarvela JN, Botsford LW. Stochastic dynamics and deterministic skeletons: population behavior of Dungeness crab. Science 1997;276:1431–5.

[101] Dennis B, Desharnais RA, Cushing JM, Henson SM, Costantino RF. Can noise induce chaos? Oikos 2003;102(2):329–39.

[102] Iansiti M, Hu Q, Westervelt RM, Tinkham M. Noise and chaos in a fractal basin boundary regime of a Josephson junction. Phys Rev Lett Aug 1985;55:746–9.

[103] Anishchenko V, Herzel H. Noise-induced chaos in a system with homoclinic points. Z Angew Math Mech 1988;68:317–8.

[104] Bulsara AR, Schieve WC, Jacobs EW. Homoclinic chaos in systems perturbed by weak Langevin noise. Phys Rev A Jan 1990;41:668–81.

[105] Gao JB, Hwang SK, Liu JM. When can noise induce chaos? Phys Rev Lett Feb 1999;82:1132–5.

[106] Billings L, Bollt EM, Schwartz IB. Phase-space transport of stochastic chaos in population dynamics of virus spread. Phys Rev Lett 2002;88:234101.

[107] Ellner SP, Turchin P. When can noise induce chaos and why does it matter: a critique. Oikos 2005;111(3):620–31.

[108] Do Y, Lai Y-C. Scaling laws for noise-induced superpersistent chaotic transients. Phys Rev E 2005;71:046208.

[109] Do Y, Lai Y-C. Extraordinarily superpersistent chaotic transients. Europhys Lett 2004;67:914–20.

[110] Hastings A, Cuddington K, Davies KF, et al. The spatial spread of invasions: new developments in theory and evidence. Ecol Lett 2005;8:91–101.

[111] Lewis MA, Petrovskii SV, Potts J. The mathematics behind biological invasions. Interdisciplinary applied mathematics, vol. 44. New York: Springer; 2016.

[112] Lewis MA, Kareiva P. Allee dynamics and the spread of invading organisms. Theor Popul Biol 1993;43:141–58.

[113] Sherratt JA, Lewis MA, Fowler AC. Ecological chaos in the wake of invasion. Proc Natl Acad Sci USA 1995;92:2524–8.

[114] Malchow H, Petrovskii SV, Venturino E. Spatiotemporal patterns in ecology and epidemiology: theory, models, and simulation. Chapman & Hall/CRC; 2008.

[115] Petrovskii SV, Malchow H. Critical phenomena in plankton communities: KISS model revisited. Nonlinear Anal, Real World Appl 2000;1:37–51.

[116] Petrovskii SV, Malchow H. Wave of chaos: new mechanism of pattern formation in spatio-temporal population dynamics. Theor Popul Biol 2001;59:157–74.

[117] Malchow H, Petrovskii SV. Dynamical stabilization of an unstable equilibrium in chemical and biological systems. Math Comput Model 2002;36(3):307–19.

[118] Dagbovie AS, Sherratt JA. Absolute stability and dynamical stabilisation in predator-prey systems. J Math Biol 2014;68(6):1403–21.

[119] Sherratt JA. Invasive wave fronts and their oscillatory wakes are linked by a modulated travelling phase resetting wave. Physica D 1998;117:145–66.

[120] Petrovskii SV, Kawasaki K, Takasu F, Shigesada N. Diffusive waves, dynamical stabilization and spatio-temporal chaos in a community of three competitive species. Jpn J Ind Appl Math 2001;18:459–81.

[121] Cangiani A, Georgoulis EH, Morozov AY, Sutton OJ. Revealing new dynamical patterns in a reaction–diffusion model with cyclic competition via a novel computational framework. Proc R Soc A 2018;474(2213):20170608.

[122] Petrovskii SV, Morozov AY, Li B-L. Regimes of biological invasion in a predator-prey system with the Allee effect. Bull Math Biol 2005;67:637–61.

[123] Petrovskii SV, Malchow H. A minimal model of pattern formation in a prey-predator system. Math Comput Model 1999;29(8):49–63.

[124] Tél T, Lai Y-C. Chaotic transients in spatially extended systems. Phys Rep 2008;460:245–75.

[125] Hastings A, Higgins K. Persistence of transients in spatially structured ecological models. Science 1994;263:1133–6.

[126] Kot M, Schaffer WM. Discrete-time growth-dispersal models. Math Biosci 1986;80:109–36.

[127] Neubert MG, Kot M, Lewis MA. Dispersal and pattern formation in a discrete-time predator-prey model. Theor Popul Biol 1995;48:7–43.

[128] Dhamala M, Lai Y-C, Holt RD. How often are chaotic transients in spatially extended ecological systems? Phys Lett A 2001;280:297–302.

[129] Hassell MP, Comins HN, May RM. Spatial structure and chaos in insect population dynamics. Nature 1991;353:255–8.

[130] Comins HN, Hassell MP, May RM. The spatial dynamics of host-parasitoid systems. J Anim Ecol 1992;61:735–48.

[131] Rodrigues LAD, Mistro DC, Petrovskii SV. Pattern formation in a space- and time-discrete predator-prey system with a strong Allee effect. Theor Ecol 2012;7:77–88.

[132] Vasconcelos DB, Viana RL, Lopes SR, de SE, Pinto S. Conversion of local transient chaos into global laminar states in coupled map lattices with long-range interactions. Physica A 2006;367:158–72.

[133] Crutchfield JR, Kaneko K. Are attractors relevant to turbulence? Phys Rev Lett 1988;60:2715–8.

[134] Kaneko K. Theory and applications of coupled map lattices. Chichester: John Wiley; 1993.

[135] Kaneko K. Supertransients, spatiotemporal intermittency and stability of fully developed spatiotemporal chaos. Phys Lett A 1990;149:105–12.

[136] Jankovic M, Petrovskii S, Banerjee M. Delay driven spatiotemporal chaos in single species population dynamics models. Theor Popul Biol 2016;110:51–62.

[137] Daufresne T, Hedin LO. Plant coexistence depends on ecosystem nutrient cycles: extension of the resource-ratio theory. Proc Natl Acad Sci USA 2005;102:9212–7.

[138] Pastor J, Walker RD, Larsson S. Delays in nutrient cycling and plant population oscillations. Oikos 2006;112:698–705.

[139] Ginzburg LR, Taneyhill DE. Population cycles of forest Lepidoptera: a maternal effect hypothesis. J Anim Ecol 1994;63:79–92.

[140] Turchin P. Complex population dynamics: a theoretical/empirical synthesis. Princeton NJ: Princeton University Press; 2003.

[141] Maynard Smith J. Models in ecology. Cambridge UK: Cambridge University Press; 1974.

[142] Kuang Y. Delay differential equations with applications in population dynamics. New York: Academic Press; 1993.

[143] Jankovic M, Petrovskii SV. Are time delays always destabilizing? Revisiting the role of time delays and the Allee effect. Theor Ecol 2014;7:335–49.

[144] Smith H. An introduction to delay differential equations with sciences applications to the life. Berlin: Springer; 2011.

[145] Bommarco R, Heikkinen RK, Helm A, et al. Extinction debt: a challenge for biodiversity conservation. Trends Ecol Evol 2009;24:564–71.

[146] Munch SB, Poynor V, Arriaza JL. Circumventing structural uncertainty: a Bayesian perspective on nonlinear forecasting for ecology. Ecol Complex 2016.

[147] MacHunter J, Wright W, Loyn R, Rayment P. Bird declines over 22 years in forest remnants in southeastern Australia: evidence of faunal relaxation? Can J For Res 2006;36(11):2756–68.

[148] Bulman CR, Wilson RJ, Holt AR, et al. Minimum viable metapopulation size, extinction debt, and the conservation of a declining species. Ecol Appl 2007;17(5):1460–73.

[149] Candeѐs E. Compressive sampling. In: Proceedings of the international congress of mathematicians, vol. 3. 2006. p. 1433–52.

[150] Baraniuk RG. Compressed sensing. IEEE Signal Process Mag 2007;24:118–21.

[151] Candeѐs E, Wakin M. An introduction to compressive sampling. IEEE Signal Process Mag 2008;25:21–30.

[152] Su R-Q, Lai Y-C, Wang X, Do Y-H. Uncovering hidden nodes in complex networks in the presence of noise. Sci Rep 2014;4:3944.

[153] Wang W-X, Lai Y-C, Grebogi C. Data based identification and prediction of nonlinear and complex dynamical systems. Phys Rep 2016;644:1–76.

[154] Wang W-X, Yang R, Lai Y-C, Kovanis V, Grebogi C. Predicting catastrophes in nonlinear dynamical systems by compressive sensing. Phys Rev Lett 2011;106(15):154101.

[155] Wang W-X, Yang R, Lai Y-C, Kovanis V, Harrison MAF. Time-series-based prediction of complex oscillator networks via compressive sensing. Europhys Lett 2011;94(4):48006.

[156] Wang W-X, Lai Y-C, Grebogi C, Ye J-P. Network reconstruction based on evolutionary-game data via compressive sensing. Phys Rev X 2011;1(2):021021.

[157] Candès E, Romberg J, Tao T. Stable signal recovery from incomplete and inaccurate measurements. Commun Pure Appl Math 2006;59(8):1207–23.

[158] Zeeman ML, Meyer K, Bussmann E, et al. Resilience of socially valued properties of natural systems to repeated disturbance: a framework to support value-laden management decisions. Nat Resour Model 2018:e12170.

[159] Scheffer M. Fish and nutrients interplay determines algal biomass: a minimal model. Oikos 1991;62:271–82.

[160] Malchow H. Non-equilibrium spatio-temporal patterns in models of non-linear plankton dynamics. Freshw Biol 2000;45:239–51.