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Regime shifts at the origin of a long transient  
methodological development for predictive ecology.  
Comment on "Long transients in ecology: Theory and  
applications" by A. Morozov *et al.*

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In the context of rapid and large-scale environmental changes, including climate change, habitat fragmentation, overfishing, biological invasions and so on, many species are under severe pressure that may lead them to extinction. The resulting loss of biodiversity may have important consequences for community structures and the functioning of ecosystems [1] and for the services they can supply to humanity [2]. In the face of these threats, effectiveness in managing the environment crucially depends on our ability to anticipate the response of communities and ecosystems to the perturbations experienced. Accordingly, an efficient environmental management must rely on accurate forecasts, while it is well recognized that ecological predictions still need to be improved [3], [4]. Regime shifts in ecological systems are particularly difficult to anticipate, and this is where the comprehensive review by Morozov *et al.* [5] comes into play.

A regime shift is a rapid and abrupt change of state of a system. Rapid declines for instance are typically encountered when populations collapse (e.g. [6]). Many papers propose methods based on [7] to detect the tipping point when it is due to a critical transition, meaning that a relatively slow change in the environment leads the system to a bifurcation (a fold point) where the state of the system becomes unstable. But there is a lack of systematic review on methods for predicting such collapses [8] or shift regimes in general. The review by Morozov *et al.* is an interesting contribution to reduce this gap by providing a comprehensive review of works that propose a more systematic frame. It refers to long transient dynamics [9] and aims at explaining why and how this general approach could shed new light on the issue raised by regime shifts prediction. Progresses in this direction would assist environmental managers to avoid wrong decisions and moreover, in some cases, to improve the anticipation of ruptures in dynamics.

Several objectives are reached in this review. First, it provides a definition

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of a long transient dynamics. Then the authors describe different mechanisms underlying long transient dynamics and how they could constitute a systematic framework for analysing time series. Finally, the question of environmental management is discussed in this context.

Since it is difficult to describe the relative slowness of a dynamic in practice, an efficient definition of long transient dynamics is not obvious to set up and it could easily be useless. However, this pitfall is avoided in this review by Morozov *et al.*. Indeed, not only the definition is here based on qualitative properties of dynamical systems but is completed by a quantitative tool as well (the time scaling law). Several illustrative examples of long transients from the literature are provided.

The review by Morozov *et al.* supplies a set of mechanisms underlying the rapid changes in dynamical systems after a long transient. Even if regime shifts have often been explained by critical transitions, which involve a change of the environment, they can actually occur spontaneously in appearance, without any modification of the environment. In this review, crawl-by and saddle points in the phase space, ghost attractors, slow-fast systems, noise, spatial dispersion and time delayed systems are gathered and organised to set up a general framework for understanding long transient dynamics and to develop tools for time series analysis and tipping points anticipation. Several examples from the literature, based on models and/or data, illustrate the relevance of the methods and show how they can be used to explain the origin of the shifts. The time scaling law is calculated and related to the fundamental parameters of the studied system in each case.

When a system is represented by a model, state variables are generally chosen because they describe some variables of interest for the system, but when processes underlying the dynamics take place on different time scales, there is often a change of variables that allows to modify the model and to write it under the form of a slow fast system, where some variables are fast and other are slow. This change of variables is sometime straightforward but it is not always the case, see [10]. As discussed in the review by Morozov *et al.*, one general property of the nonspatial models exhibiting long transient is the existence of a small parameter. Using this property to find a change of variables that would exhibit the slow fast form of the model would be useful for analyzing the model and unravelling its dynamics. Indeed, the study of a slow fast system uses the asymptotic properties of the fast system to understand the transient dynamics of the whole model. In other words, from a technical point of view, all the tools developed for studying asymptotic dynamics are now available and helpful for analysing transient dynamics. In this context, regime shifts often result from a bifurcation in the fast part of the system (but as far as I see, ghost attractors come out this frame). Thus works on the dynamical consequences of bifurcations in the fast dynamics have to be developed (see [11] for a recent review of existing methods).

When time series are available, confusion between the mechanisms driving the dynamics is easy. As an example, let us consider the case of competition between fly species described in [12]. In this situation, the crawl-by could explain

the dynamics as illustrated on (1), where a Lotka-Volterra model is used. The trajectory follows the stable manifold of a saddle point (extinction of *Phaenicia sericata*) and then jump to a stable node (extinction of *Musca domestica*). However, it is well known that *M. domestica* is more competitive than *P. sericata* but the authors in [12] set an experimental design that gave the data in Figure 1. A more likely explanation here would be that selection comes into play, the low density of *P. sericata* constrains the species to more interspecific interactions while *M. domestica* often meets intraspecific interactions. After several weeks, selection could lead to more competitive individuals of *P. sericata*. Here, a slow fast model with fast population dynamics and slow interspecific competition traits driven by adaptation/selection processes would also lead to such a dynamics. More generally, regime shifts in population abundances can follow shifts in factors like individual traits (genotype, phenotype, or other types of traits) and these are not always visible in the observed data. A slow drift in the internal structure of the population may then result in a rapid change in the population density and such an indirect mechanism is not always easy to unravel if not suspected. However, with this in mind, a slow fast model can be developed to reproduce both the internal structure (slow dynamics) and the population density (fast variable) and of course data are needed to support the model choice: the model can prove to be useful here to set up the observation strategy.

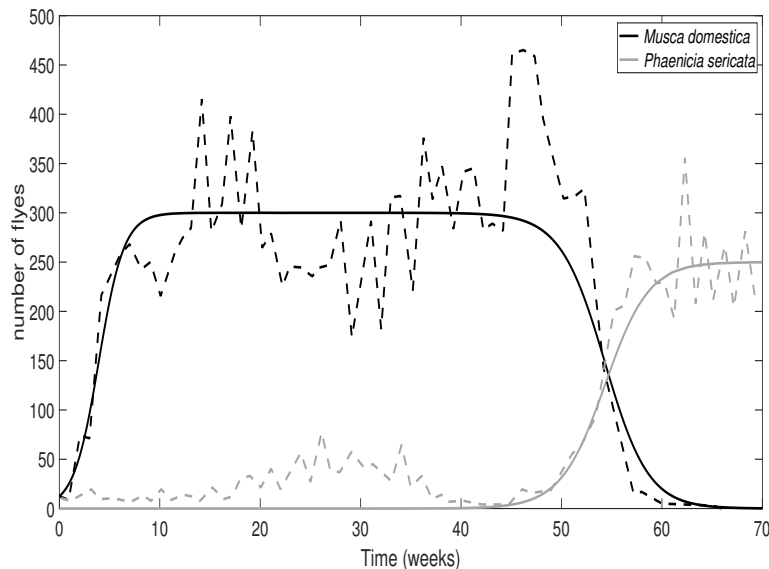


Figure 1: Long transient dynamics in a competition system with two fly species in an experiment design, *Musca Domestica* in black and *Phaenicia sericata* in grey. A Lotka-Volterra competition model (full lines) is used and compared to data (dashed lines) from [12]. In this figure, a crawl-by explains the rapid change of dominant species occurring after 50 weeks.

95 Therefore, from a general management perspective, the first step consists  
in identifying the generic mechanisms associated to observations, and then to  
determine a relevant procedure to avoid a shift before its occurrence, if possi-  
ble. The review by Morozov *al.* sets the basis for the first step, but of course  
methodological developments are still required. Among them, a set of statisti-  
100 cal tests associated to models and dynamical systems theory, in the same line  
as it has been done in [13], would help managers to discriminate between the  
different mechanisms and to take pertinent decisions. In conclusion, the review  
by Morozov *et al.* is a clear and interesting contribution for addressing the  
substantial challenged raised by ecological regime shifts.

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135