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Impact of seasonal forcing on reactive ecological systems

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ABSTRACT

Our focus is on the short-term dynamics of reactive ecological systems which are stable in the long term. In these systems, perturbations can exhibit significant transient amplifications before asymptotically decaying. This peculiar behavior has attracted increasing attention. However, reactive systems have so far been investigated assuming that external environmental characteristics remain constant, although environmental conditions (e.g., temperature, moisture, water availability, etc.) can undergo substantial changes due to seasonal cycles. In order to fill this gap, we propose applying the adjoint non-modal analysis to study the impact of seasonal variations of environmental conditions on reactive systems. This tool allows the transient dynamics of a perturbation affecting non-autonomous ecological systems to be described. To show the potential of this approach, a seasonally forced prey-predator model with a Holling II type functional response is studied as an exemplifying case. We demonstrate that seasonalities can greatly affect the transient dynamics of the system.

1. Introduction

A dynamical system exhibits a stable equilibrium configuration when small disturbances decay to zero after a sufficiently long time from their onset. However, perturbation temporal dynamics occurring at finite time can exhibit two types of behavior. Perturbations can either monotonically decay to zero or exhibit large and long lasting *transient amplifications* before disappearing (Schmid and Henningson, 2000). In the former case, the short-term and the long-term qualitative dynamics coincide. In the latter case, the system state can transiently run very far from the final equilibrium configuration, and the complete recovery of the equilibrium may take a great deal of time. This non-monotone decay of perturbations has important consequences. Firstly, when the timescales of interest are shorter than the duration of the transient amplifications, the system appears unstable (i.e., disturbances amplify) although perturbations disappear after a long time. Secondly, external perturbations may repeatedly force the system, thus keeping the system away from the equilibrium configuration. Thirdly, disturbances can amplify to such an extent that they render the nonlinear terms significant. If this occurs, secondary instabilities can be triggered (the so-called by-pass transition, see (Rempfer, 2003; Lee and Wu, 2008)).

The occurrence of transient amplifications in asymptotically stable dynamical systems was detected for the first time in the field of hydrodynamic stability (Trefethen et al., 1993; Reddy and Henningson, 1993). Soon after, transient growths were also found to play a crucial role in other problems, such as laser physics (Siegman, 2001, 1986), the numerical solution of nonlinear partial differential equations (Trefethen and Embree, 2005), and geophysical morphodynamics (Camporeale and Ridolfi, 2009; Vesipa et al., 2012; Caruso et al., 2016). Transient amplifications of the total perturbation energy are possible only when the eigenvectors of the corresponding linearized system are non-orthogonal (Arnoldi et al., 2016; Trefethen and Embree, 2005). For this reason, studies about the short-term behavior of perturbations in stable dynamical systems are often referred to as non-normal or non-modal analyses. However, it should be stressed that the non-normality of the eigenvector set is a necessary but not sufficient condition to induce the transient growth of perturbations (Trefethen and Embree, 2005).

In ecology, the dynamics of populations were investigated for the first time from a non-modal perspective by Neubert and Caswell (1997). They demonstrated that strong transient growths of population perturbations can occur in ecological systems, and defined as *reactive* those systems which exhibit transient amplifications. As the short-term response of a reactive stable system (i.e., amplification of perturbations) is completely different from its asymptotic behavior (i.e., damping of perturbations), Neubert and Caswell (1997) highlighted that non-modal analysis is fundamental to understand and interpret the dynamics observed in the real world. In fact, reactive ecological systems are continuously perturbed by external disturbances, and real world dynamics are likely to be a sequence of short-term responses triggered by environmental perturbations.

The seminal work by Neubert and Caswell (1997) opened the way to the non-modal stability analysis of ecological problems. The occurrence

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of transient growth of perturbations was found to be a key property in discrete-time ecological systems (Caswell and Neubert, 2005), matrix population models (Caswell, 2001), food webs (Chen and Cohen, 2001), prey-predator models (Neubert et al., 2004), and ecosystem compartment models (Marvier et al., 2004). More recently, Caswell (2007) and Verdy and Caswell (2008a) focused on sensitivity analyses of transient population dynamics. Anderson et al. (2008) extended the transient response analysis to advective systems, while Buckwar and Kelly (2014) considered the impact of stochastic disturbances. Many studies have also been devoted to understanding the ecological causes of the transient growth of perturbations (Verdy and Caswell, 2008a; Snyder, 2010) and to developing a theoretical framework for finding transient growths in ecological time-series obtained from experiments (Neubert et al., 2009). Several experiments and field observations have confirmed the existence of transient growths in real ecological systems, such as populations of flour beetles of the genus *Tribolium* (Caswell and Neubert, 2005; Cushing, 2003) and plant populations (Stott et al., 2010; Ellis and Crone, 2013). Finally, the study of transient growth of perturbations has become an important issue in population management (Ezard et al., 2010).

The relation between *reactive* systems and *excitable* systems has also been explored (McCoy, 2013). In reactive stable systems, infinitesimal perturbations can be transiently amplified. On the other hand, in excitable stable systems only finite-amplitude perturbations are important. If the size of a perturbation exceeds a given threshold, the perturbation experiences long and strong amplification phenomena (Truscott and Brindley, 1994; Morozov and Petrovskii, 2009). In contrast, monotonic decay is observed if the size of perturbations is below the threshold. Reactivity is a purely linear phenomenon, while excitability is related to nonlinear dynamics. Hence, reactivity and excitability are conceptually unrelated: there are reactive systems that are not excitable and vice versa (McCoy, 2013). However McCoy (2013) demonstrated that many systems which exhibit excitable dynamics also display a strong reactivity, in the same regions of the parameter space.

A common assumption adopted in previous studies about reactive system is that the environmental conditions are constant during the onset and the evolution of perturbations. One remarkable exception is the work by Caswell (2007), which showed some preliminary results about time-varying discrete models. However, it is well known that many ecological systems are sensitive to cyclical environmental conditions, e.g., the alternation of day and night, seasons, tides, etc. These cycles induce periodic temporal variations in physical and environmental characteristics (e.g., temperature, moisture, light, water availability, visibility, etc.). As a result, periodical oscillations of ecological parameters that regulate population dynamics arise. Examples of these are: oscillations in the birth or death rate, in the time predators take to find their prey, in the availability of food, etc. (e.g., Cushing, 1977; Kuznetsov et al., 1992).

Seasonalities can have a great impact on population dynamics (hereafter we will use the word seasonality to refer to a cyclic variation of an ecological parameter irrespective of the cycle length). Seasonalities are, in fact, responsible for the occurrence in population dynamics of forced stable cycles, multiple attractors and subharmonics, catastrophic transitions, phase-locking, quasi-periodic behavior, and chaos (Cushing, 1977; Kuznetsov et al., 1992; Rinaldi et al., 1993; Summers et al., 2000; Selgrade and Roberds, 2001; Franke and Selgrade, 2003). Seasonalities also affect the persistence of populations in prey-predator systems, as shown by, among others, Baek (2009); Baek et al. (2009); Garrione and Rebelo (2016). Finally, seasonal oscillations are critical in real world problems, such as phytoplankton evolution (Pascual, 1994), insect population dynamics (Henson and Cushing, 1997), the bio-economics of renewable resources (Castilho and Srinivasu, 2007), the control of apple snails (Zhang and Zhu, 2007), the dynamics of microorganisms subject to sequences of nutrient and antibiotic inputs (Zhang and Chen, 2008), and fish population dynamics in lakes with oscillating level (Moussaoui et al., 2015).

The general picture is that, on the one hand, the study of reactive systems has attracted much interest, but only the autonomous case has been considered (i.e., model parameters are time independent). On the other hand, periodic oscillations of environmental conditions are widespread and can affect the system dynamics to a great extent. In this scenario, two questions arise: Are the short-term dynamics of reactive systems affected by a seasonal environmental forcing? And, if so, to what extent? This topic has not been explored and is the focus of our work.

In order to analytically study the transient behavior of seasonally forced ecological systems, we propose applying non-modal adjoint analysis (Schmid, 2007). This mathematical technique allows the study of the full evolution of perturbations (i.e., from the onset at $t=0$ to the eventual dissipation for $t \to \infty$) evaluating the so-called growth function. This function embeds and completes the information that can be obtained by the assessment of the reactivity alone, which only focuses on the maximum growth rate of a perturbation at $t=0$ (Neubert and Caswell, 1997; Arnoldi et al., 2016).

We restrict our analysis to seasonal oscillations characterized by a long duration with respect to the typical intrinsic timescales of the ecological system. This allows us to describe the basic non-autonomous dynamics of the unperturbed system as a succession of equilibrium states (i.e., unperturbed populations adjust instantaneously to new environmental conditions).

In order to show the impact of seasonalities on reactive systems, the proposed approach will be applied to a typical prey-predator model with a Holling II type prey-predator response. This model was introduced for the first time by Bazykin (1976) and is often referred to in the literature as the Rosenzweig-MacArthur (RMA) prey-predator model (Rosenzweig and MacArthur, 1963). This model, widely used in a great number of previous studies, represents a wide class of real systems (Verdy and Caswell, 2008b; Hilker and Lewis, 2010; Sherratt et al., 2014; Garrione and Rebelo, 2016), and was extended to include seasonalities of the ecological parameters (Rinaldi et al., 1993). Thus, the RMA model provides an excellent case study to investigate how a seasonally varying environment affects the transient amplification of perturbations.

In the next section, the conceptual and analytical tools adopted to study the short-term response of non-autonomous dynamical systems are described. The third section is devoted to recalling the seasonal RMA model, and to applying the non-modal adjoint analysis. Finally, the effect of seasonalities on the short-term dynamics of predator and prey populations is shown in Section 4. It should be noted that our results are focused on the RMA model, but the proposed approach can be applied for studying the short-term dynamics of any seasonally forced ecological system.

2. Transient dynamics in ecological systems with time-dependent parameters

Competitive communities, spatially structured populations, species interacting in a food web, or abiotic-biotic flows in ecosystem models are typically described by non-linear dynamical systems in continuous time (Arnoldi et al., 2016). In these problems, species biomasses (or number of individuals) are the dependent system variables. Let us consider a generic case in which N variables interact in a seasonally varying environment according to the set of N coupled differential equations

$$\frac{\mathrm{d}\mathbf{Q}(t)}{\mathrm{d}t} = \mathbf{g}[\mathbf{Q}(t), f(t)], \qquad (1)$$

where the vector $\mathbf{Q}(t)$ collects the dependent variables, the N-dimensional function $\mathbf{g}$ describes the biomass dynamics and the species interaction, and $f(t)$ is the time-dependent forcing. This external forcing represents the impact of the time-dependent external environmental conditions on the ecological system, and renders the dynamical