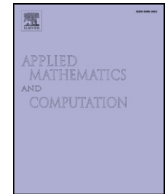




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Separatrix reconstruction to identify tipping points in an eco-epidemiological model

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ABSTRACT

Many ecological systems exhibit tipping points such that they suddenly shift from one state to another. These shifts can be devastating from an ecological point of view, and additionally have severe implications for the socio-economic system. They can be caused by overcritical perturbations of the state variables such as external shocks, disease emergence, or species removal. It is therefore important to be able to quantify the tipping points. Here we present a study of the tipping points by considering the basins of attraction of the stable equilibrium points. We address the question of finding the tipping points that lie on the separatrix surface, which partitions the space of system trajectories. We present an algorithm that reconstructs the separatrix by using a Moving Least Squares approximant based on radial basis functions. The algorithm is applied to an eco-epidemiological model of pack hunting predators that suffer disease infection. Our analysis reveals that strong hunting cooperation considerably promotes the survival of predators and renders the predators resilient to perturbations.

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1. Introduction

Many ecosystems can be found in one of several possible alternative stable states [6,25,27,28,33,36,38]. Consequently, such ecosystems can shift abruptly from one state to another—a phenomenon also known as ecological regime shift. Well-known examples include shifts from clear to turbid waters [10], from grassland to shrubland [34], the collapse of fisheries [32], and the degradation of coral reefs [30]. As regime shifts often imply catastrophic consequences for the ecosystem, failure to recognize alternative stable states or wrong predictions of the threshold points between them can turn out not only as a surprise, but also costly.

Regime shifts can be triggered by perturbations of the state variables or by changing parameters [6,29,35]. In the latter case, environmental drivers typically lead to the appearance (or disappearance) of alternative stable states and thus cause sudden shifts. In the former case, the ecosystem is already multistable, and an overcritical disturbance of the state variables shifts the system from the basin of attraction of one stable state to the basin of attraction of another stable state. The basins of attraction are separated by a separatrix, which corresponds to threshold values of the state variables, also called tipping points.

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In a simple system with one state variable only, the tipping point corresponds to the unstable equilibrium that separates two stable steady states. However, in higher dimensional systems, information about the separatrix is needed. In particular, the tipping point of a certain state variable is not a single value for a given set of parameters anymore, but it depends on the values of the other state variables as the separatrix is a higher dimensional object.

Knowledge of the existence and location of tipping points is fundamental for understanding and managing ecosystems [9,10,23,36]. Yet, theoretical ecology rarely addresses the identification of tipping points in higher dimensional systems. There is a need of methods that help in accomplishing this task. In this paper, we provide a numerical tool to locate the tipping points of a higher dimensional system. The idea is to approximate the surface that partitions state space into the two different domains of attraction, i.e. the separatrix. In [11–13] the authors divide the points in the state space into different regions depending on where the trajectories stabilize. We propose an algorithm that is able to find the points of the separatrix by limiting the search area, and we propose an alternative method to reconstruct the separatrix surface using a Moving Least Squares approximant [18,26]. This quasi-interpolant is formulated by means of radial basis functions with compact support, providing a local approximation of each evaluation point. This method, using the explicit formula of the Lagrange multipliers, avoids the setting up of a large interpolation system, thus reducing the computational cost.

We apply our method to find the tipping points of an eco-epidemiological model proposed in [24]. This model combines disease transmission in a predator population with the ecological dynamics of a predator–prey system. The feature of this model is that predators cooperate by hunting in packs. This cooperation can induce a tipping point in the predator density: if predator density is too small, the predator population goes extinct as they are not sustained by the prey. However, if the predator density is large enough, hunting cooperation mediates predator survival due to increased prey consumption. The critical predator density needed for survival corresponds to the tipping point between extinction and persistence. In ecology, this tipping point is also known as extinction threshold or as Allee threshold [7,8,15]. The Allee effect describes the positive correlation between population density and population fitness (measured as the per-capita growth rate) [3,15]. There are two types of Allee effects. Strong Allee effects are characterized by a critical threshold below which populations go extinct, whereas weak Allee effects do not induce a threshold such that small populations can survive. We will use our method to study how the Allee threshold changes for varying ecological and epidemiological parameters. We will find that the strong Allee effect can turn effectively into something similar to a weak Allee effect, of which we become aware only because we approximate the Allee threshold.

In the next Section, we introduce the eco-epidemiological model and summarize the main results on its dynamical behavior. In Section 3 we explain the algorithm developed to reconstruct the separatrix manifold, and in Section 4 we apply the algorithm to the eco-epidemiological model. The final section presents conclusions and some ideas for future work.

2. Eco-epidemiological model

In this section, we recap an eco-epidemiological model introduced and analyzed in [24]. This model exhibits bistability and will be used to illustrate the numerical tool to approximate separatrix surfaces later on.

In many biological systems animals exhibit social behavior. Pack-hunting animals are an example, where predators hunt their prey by working together with other members of their species. For example, African wild dogs [16,17] organize themselves in a coordinated formation to surround and attack their prey. Lions hunt in pack of three to seven individuals, splitting into center and wings, to ambush prey [37]. Cooperation in a group represents a mechanism developed through evolution to improve the skills of hunting and the chance of survival.

In the last decades, biomathematics has paid increasing attention to social behavior as it is well known to induce strong Allee effects. Thus, there is the possibility of extinction if population density falls below the critical value known as Allee threshold [5,15,22,24,39]. Therefore it is important to study this quantity in order to protect endangered species (or to guide eradication campaigns of pest species). Population dynamics can be modeled mathematically by means of a system of differential equations with the population densities over time as unknowns and with suitable parameters to describe population interactions such as predation. The mathematical approach coupled with experimental investigations allows to convert the underlying mechanism into a predictive science [31].

The eco-epidemiological model considered here is based on prey and predator populations with densities N and P , respectively. Predators are assumed to be cooperative hunters and to suffer an infectious disease, which is why the predator population is split into susceptibles (S) and infecteds (I), with $P = S + I$. The population dynamics in time T can be described by a three-dimensional system of nonlinear ordinary differential equations:

$$\begin{aligned}\frac{dN}{dT} &= r \left(1 - \frac{N}{K}\right) N - (a_0 + a_1 P) NP, \\ \frac{dS}{dT} &= -\beta \frac{SI}{P} - mS + \epsilon (a_0 + a_1 P) NS + (1 - \theta) \epsilon (a_0 + a_1 P) NI, \\ \frac{dI}{dT} &= \beta \frac{SI}{P} - mI - \mu I + \theta \epsilon (a_0 + a_1 P) NI.\end{aligned}$$

We assume logistic growth in prey, with r being the per capita net growth rate and K the carrying capacity. Predators have a natural per capita death rate m and grow by consuming prey. Their functional response to prey is given by the term

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