Bifurcation analysis of an agent-based model for predator–prey interactions

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ABSTRACT

The Rosenzweig–MacArthur model is a set of ordinary differential equations (ODEs) that provides an aggregate description of the dynamics of a predator–prey system. When including an Allee effect on the prey, this model exhibits bistability and contains a pitchfork bifurcation, a Hopf bifurcation and a heteroclinic bifurcation. We develop an agent-based model (ABM) on a two-dimensional, square lattice that encompasses the key assumptions of the aggregate model. Although the two modelling approaches – ODE and ABM – differ, both models exhibit similar bifurcation patterns. The ABM model's behaviour is richer and it is analysed using advanced statistical methods. In particular, singular spectrum analysis is used to robustly locate the transition between apparently random, small-amplitude fluctuations around a fixed point and stable, large-amplitude oscillations. Critical slowing down of model trajectories anticipates the heteroclinic bifurcation. Systematic comparison between the ABM and the ODE models' behaviour helps one understand the predator–prey system better; it provides guidance in model exploration and allows one to draw more robust conclusions on the nature of predator–prey interactions.

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1. Introduction and motivation

Ecologists are more and more frequently asked to make predictions about the potential effects of specific changes to an ecosystem or a community of species. This demand is particularly vivid in the context of climate change (Lavergne et al., 2010; Valladares et al., 2014) or resource management. It especially applies when anthropic harvesting is at play, as in fisheries (Lindegren et al., 2010), or when biological factors might disturb an established community of species, as in cases of non-endemic species invading an ecosystem (Crowl et al., 2008). Understanding these consequences is also relevant when the driver of changes is internal, in particular through evolutionary processes (Ferrière, 2009).

Whether the engine of change is external or internal, analysing the consequences requires a comprehensive understanding of the community dynamics. Achieving such an understanding has proven to be a challenging task. Observational and experimental data show that an ecological system composed of only two interacting species can exhibit non-trivial dynamics, such as bistability and oscillations (e.g., Fussmann et al., 2000). The importance of non-linear mechanisms in leading to such dynamics has motivated theoretical work on simple models to characterise the dynamical regimes, identify and circumscribe basins of attraction, and locate bifurcations or regime shifts. To do so, ecologists have borrowed mathematical concepts and tools from other disciplines and tried a variety of modelling techniques, especially using systems of ordinary differential equations (ODEs).

A recent innovation is the development of agent-based models (ABMs), also called individual-based models in the ecological literature. ABMs simulate systems described by the rules of interaction among autonomous individuals. According to DeAngelis and Mooij (2005), some scholars view ABMs as exploratory tools that extend classical aggregate models, whereas others suggest that ABMs provide a methodological basis on which to build a novel research paradigm (Grimm et al., 1999; Grimm and Railsback, 2005). In the field of population dynamics, ABMs have helped investigate the role of local interactions (Mccauley et al., 1993) and spatial dynamics (Dieckmann et al., 2000); they are also being increasingly employed to study evolutionary dynamics (Łomnicki, 1999; Gras et al., 2009).

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Can ABMs help the understanding of community dynamics? How can their use complement the classic ODE approach? In climate sciences, it has been proposed to advance knowledge by moving across a hierarchy of models of the same class of phenomena (Schneider and Dickinson, 1974; Ghil, 2001; Dijkstra and Ghil, 2005). This hierarchy ranges from low-resolution 'toy' models, which help understand the general behaviour of the system, all the way to very detailed 'realistic' models, which may be used for real-time forecasting of weather or climate. Moving up the hierarchy implies adding mechanisms and improving resolution, which often comes at the cost of losing analytical tractability and insight. Detailed models have to be integrated numerically, and analysing their outputs may require complex statistical manipulations. Going back and forth between different levels allows one to test the robustness of the conclusions and guide fruitful improvements of the models at each level of the hierarchy.

The hierarchical modelling approach could be insightfully applied to study the dynamics of communities and even ecosystems. It would thus appear that classical ODE systems, such as the Lotka–Volterra equations, are toy models – in the hierarchical modelling terminology (Ghil, 2001) – whereas the ABM framework is more appropriate for developing detailed models. ABMs can be seen as more realistic, since agents often correspond to observable organisms (Bonabeau, 2002). Contrasting the results of different models has already allowed ecologists to point out some mechanisms that a single-model approach may overlook, such as the influence of spatial distribution and localised interactions (Donalson and Nisbet, 1999; Durrett and Levin, 1994), of physiological structure (De Roos and Persson, 2005) and of heterogeneity (Hastings, 1990). In particular, Dieckmann et al. (2000) pointed out instances in which the dynamics of mean-field models differ from the ABMs they derive from, and proposed new mathematical methods to integrate the spatially distributed aspects of ABMs into ODEs, such as moment methods (Law and Dieckmann, 2000) or pair-wise approximations (van Baalen, 2000).

In this paper, we illustrate the hierarchical modelling approach by revisiting a classical predator–prey system and comparing the dynamical behaviour of an ABM with that of an ODE model. The guiding thread of this comparison is to determine whether the two models' bifurcation patterns – which summarise the key features of a system's dynamics – are qualitatively similar, even though each model is built upon distinct and complementary principles.

The key components of ODE models are the macro-level feedback mechanisms. Individuals, as distinct entities, do not play any role per se. The dynamics results from the relative abundance of each population, expressed through the principle of 'mass-action'. In ABMs, the system-level dynamics results from the micro-level actions of autonomous individuals. They follow rules, but their effective actions depend on local contingencies. In addition, agents may have only limited information on the system they are embedded in. Grimm and Railsback (2005) argue that reproducing results of a classical ODE model with ABMs often led to the design of models that are incomplete, not robust, and therefore lacking in interest.

In this paper, we do not aim to reproduce the outputs of an ODE model with an ABM, neither do we want to perform any quantitative comparison. Our objective is to establish whether the behaviour patterns of the two models are in qualitative agreement, i.e., whether the solution types – bistable, oscillatory and irregular – are in one-to-one correspondence, including the transitions between these regimes of behaviour, as long as the two models, while conceptually different, rely on the same key assumptions about the system under scrutiny. In addition, we are interested to find out – provided there is a good correspondence in regime types and bifurcations between the aggregate ODE model and the ABM – whether ideas on early warning that were developed for ODE

models Scheffer et al. (2009) can help formulate such early warnings for ABMs.

The qualitative comparison between our ODE model and the ABM is carried out by computing the corresponding bifurcation diagrams of the two models. To do this, we need to locate the bifurcation points in our ABM. The identification of attractors has not been the main emphasis of ecological ABM studies, which tend to focus instead on the emergence of spatial patterns (Grimm and Railsback, 2005; Railsback and Grimm, 2011). Analysing attractor types and the transitions between them as significant model parameters change – i.e., studying the models' bifurcations – is quite helpful in understanding regime shifts. These shifts are crucial ecological phenomena and applying bifurcation-theoretical methods to ABM studies thus follows the call of Scholl (2001) to tighten connections between agent-based modelling and dynamical systems theory. In particular, we propose and apply a method to detect the transition between regular oscillations and irregular fluctuations around a steady state.

In Section 2.1, we present the behaviour of a classical ODE model of predator–prey systems: the Rosenzweig–McArthur model with strong Allee effect on the prey. In Section 2.2, we formulate an ABM in which the key mechanisms that enter the aggregate model emerge spontaneously; these mechanisms include the functional response and the Allee effect. We then define, in Section 2.4, the experimental protocol of the simulations and explain the methods we use to analyse the resulting ABM model.

In Section 3, we present the results and compare the bifurcation diagrams obtained for the two models, while focussing on the Hopf bifurcation in Section 3.2 and on the heteroclinic one in Section 3.3. In Section 4, we explore early-warning signals for the global transitions and test them when endogenous processes or exogenous forcing modify slowly the model parameters. Finally, we discuss the methodological implications of our work within ABM studies.

2. Models and methodology

2.1. The aggregate model and its behaviour

We study the Rosenzweig–McArthur model with strong Allee effect on the prey. Boukal et al. (2007) analysed how the 'route to collapse' featured in Rosenzweig–McArthur models is influenced by the addition of either a weak or a strong Allee effect, and by the sigmoidicity of the functional response. The system's collapse occurs through a global bifurcation, characterised by an heteroclinic orbit (van Voorn et al., 2007). Wang et al. (2011) performed a rigorous analysis of the model, and focussed on the existence and uniqueness of limit cycles after the Hopf bifurcation. González-Olivares et al. (2006) performed a similar analysis with an Holling type III functional response.

Let X denote the prey population and Y the predator population. The dynamics is governed by the following two coupled ODEs:

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{K}\right)(X - A) - \alpha\frac{X}{X + S}Y, \tag{1a}$$

$$\frac{dY}{dt} = \rho\alpha\frac{X}{X + S}Y - dY. \tag{1b}$$

This model has seven parameters, whose definitions and values are listed in Table 1. We will also use $\mathbf{Z}(t) = (X(t), Y(t))$ to denote the state of our two-species ecosystem as a function of time t.

The model's dynamics can be summarised in a two-dimensional regime diagram usually plotted in the (d, A)-plane; see, for instance, González-Olivares et al. (2006), Boukal et al. (2007) and van Voorn et al. (2007). We choose ρ instead of d, which leads to a very similar diagram, plotted here as Fig. 1. The regime boundaries between regions (1) and (2) and between regions (2) and (3) were obtained