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Regime shifts caused by adaptive dynamics in prey–predator models and their relationship with intraspecific competition

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ABSTRACT

The paper concerns with regime shifts between multiple attractors in ecological predator–prey models and hysteresis phenomena caused by evolution. We present a survey of eco-evolutionary models with an adaptive trait affecting the prey defence or activity that influence predator functional response and give overview of typical consequences of the trait evolution to the predator–prey dynamics together with important references to related adaptive dynamics research. The selection and mutation process is modelled by a resident-mutant model (possible mutant invasion into a monomorphic resident population). Model derivations are given in detail for all of the common functional responses (Holling's type I, II, III and generalized). Different types of adaptive trait value dependences with respect to transient dynamics are distinguished according to the effect to the eco-system: we prove that if the prey adaptive trait evolution influence only the functional response of the predator, stable dynamics and irreversible abrupt regime changes are typical, whereas reversible regime shifts or more complex dynamics caused by adaptivity of the prey trait occur for trait adaptations that bring an advantage against predator together with intraspecific competition asymmetry. We confirm possibility of hysteresis eco-evolutionary cycle, persistent oscillations between different attractors of the ecological subsystem driven by adaptive trait dynamics.

1. Introduction

Population dynamics is an important part of biology. Population growth and ecological interactions are still studied throughout last decades enormously although the basic principles and ideas are known for more than a century. The fundamental works that concern the laws of exponential and logistic population growth of one-species populations or the basic interaction models have been modified, generalized and reformulated many times. Google Scholar returns almost 5 million links for the search phrase "population growth model"! A considerable part of the research on population dynamics addresses the question of the determinants of population growth and of the interactions among populations. Apart from this general qualitative approach more specific models are used, especially for the purposes of management and control, see e.g. coral-algae growth models (Mumby et al., 2007)), specific food-chain models (Kuznetsov et al., 2001) and so on. New effective technologies allow us to study individual-based models, see e.g. Grimm et al. (2003) and to accomplish computer simulation models as in e.g. Boit et al. (2012).

A typical system that describes a dynamical population model (when spatial distribution is omitted) is a system of parameter dependent ordinary differential equations

$$\dot{n} = \phi(n, a), \tag{1}$$

where n is a population density vector of species in the ecosystem and a is a vector of parameters as birth rates of particular species, their carrying capacities and so on. There is a plenty of studies of such systems that analyse dependence of the long-term behaviour on parameters (see e.g. Boukal et al., 2007; Kar, 2006; Mohammed et al., 2018; Mumby et al., 2007; Rinaldi et al., 1993; Scheffer et al., 1997 and many others). These works give insight to the principles involved, give possibilities to manage and control the systems, but also show that rapid changes and unexpected behaviour can happen. As a good and well-known example may serve the spruce budworm model introduced in Ludwig et al. (1978) that explains hysteresis loops in the dynamics of the population density of the budworm or variety of prey–predator models with stable limit cycles (Abrams and Walters, 1996; Boukal et al., 2007; Rosenzweig and MacArthur, 1963; Steele and Henderson,

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1992 and others). Besides the multiple equilibria and the limit cycles, more complex behaviour can be observed in some models: multiple cycles and other attractors are studied in e.g. González-Olivares and Rojas-Palma (2011) and the presence of chaotic dynamics in ecological models is shown in some ecological models (see e.g. Hastings and Powell, 1991; Huisman and Weissing, 2002; Kuznetsov et al., 2001).

Evolution as a change in the inherited traits of biological populations give the species possibility to adapt to their environments by means of natural selection. During the last two decades techniques based on game theory were developed and they are referred to as adaptive dynamics techniques (see e.g. Dercole and Rinaldi, 2008; Dieckmann and Law, 1996; Geritz et al., 1997; Metz et al., 1995). They link population dynamics to evolutionary dynamics for understanding the long-term ecological and evolutionary consequences of small mutations in the traits expressing the phenotype. Although the adaptive dynamics theory is still in development (for new results see e.g. Della Rossa et al., 2015; Dercole, 2005; Dercole, 2016; Dercole et al., 2016; Geritz et al., 2016), already obtained results have often been surprising and have given a very promising insight into the complexity of nature. There are also possibilities to use the adaptive dynamics techniques in other fields as economics, since for example innovations of products may be viewed as adaptive traits and the market equilibria existence and stability depend on the innovation dynamics (see Dercole et al., 2008).

In this paper an ecosystem (1) is considered in this eco-evolutionary context. The species are affected by adaptive change in the trait that creates feedback between the evolutionary and population dynamics. Generally, the adaptive changes in traits are described by so called canonical equation (Dieckmann and Law, 1996), a system of equations

$$\dot{x} = \varepsilon g(n, a, x), \tag{2}$$

where x is generally a vector of traits of the resident species. Hereafter, only one main trait is considered, so the equation is scalar. The evolution process does not have the same timescale as the population dynamics, so the parameter $\varepsilon > 0$ scales the rate of evolutionary change. Usually $\varepsilon \ll 1$ and Eq. (2) is slow with regard to the ecological timescale of Eq. (1). Function g is explained in more detail in the next section, for now it is enough to mention that it covers the feedback of the population dynamic process and that it is generally nonlinear. This feature is responsible for bifurcations.

Bifurcations connected to adaptive trait can be responsible for regime shifts in ecosystem (1). Trait value x may affect the vector parameter a and so it can be (at least locally) considered as a function $a = a(x)$. The trait value influences the population dynamics throughout this dependence. If ecosystem (1) reaches a stable equilibrium for a specific trait value x_r of the monomorphic resident population, the system stays at the stable equilibrium until that trait value belongs to an evolutionarily stable strategy. This condition may be violated and the feedback between population and adaptive dynamics can cause transitions from one regime to another (Dercole, 2003), abrupt and unexpected changes of population densities (Dercole, 2005; Parvinen, 2005), diversification of the species to polymorphic populations (Dercole et al., 2016; Gallien et al., 2018; Landi et al., 2013 or Hui et al., 2017) and so on.

In this study we focus on monomorphic populations with slow adaptive change of the trait that is strongly connected to some parameters of the population dynamic model (1). Of course that it is not sufficient to answer even basic questions about the persistence of the population or its stabilization at some equilibrium or attractor by analysis of the eco-system alone if mutations are taken into account (for example in Dercole et al., 2003; Landi et al., 2013 Rosenzweig-MacArthur model was transformed into a resident-mutant model by adding a third equation for the mutant population and it was shown that the evolutionary model is much richer than the resident population model). The aim of this survey is not only to present different types of ecological regime transitions between multiple ecological attractors caused by adaptive dynamics, but also to distinguish typical cases when ecosystem stays stable and when the evolution causes reversible or irreversible transients. We prove that for one specialized adaptive trait changes (for example if the trait adapts specially to prevent the prey against predators and does not significantly affects other parameters of the ecosystem), only the stable case or an irreversible regime shift is possible, whereas reversible regime shifts or more complex dynamics caused by adaptivity of the prey trait occur for trait changes that bring in advantage against predator together with intraspecific competition asymmetry.

The analysis of a population dynamic model is, of course, a first step to understand the long-term behaviour of an ecosystem, especially in cases of more complex dynamics with multiple or chaotic attractors. Quasi-equilibria and quasi-attractors of the fast subsystem are essential, but the transitions between them depend on the adaptive dynamics (the slow system) strongly. Generally, the trait values are not the parameters of the population dynamic model, but the parameters are functions of the trait values. Adaptive dynamics works according to evolutionary game theory principles and that explains why additional slow nonlinear equations give feedback to the population dynamics. The slow dynamics shift the parameters of the fast population dynamic subsystem that tends to stabilize on quasi-attractors, but different types of regime transitions may happen. These transitions are not the same as the transitions caused by parameter shifts at the population dynamic subsystem (usually described by bifurcation diagrams of population models). As a prototype example of an evolving community, a prey–-predator community with multiple attractors at the population dynamic subsystem is taken. The adaptive dynamics involve one trait of the prey that affects the parameters of the functional response of the predator. Such a model serves as a good demonstrative example, because the modelled situation is easy to imagine and also to explain. One may imagine the mutant prey phenotype change as getting stronger through a genetic mutation and selection process and therefore the new resident prey with adapted trait is able to defend itself more effectively from a predator. It is clear from this example, that the handling time, the encounter rate parameters or other parameters in the functional response may be influenced and varied by the trait value. This parametric change may significantly affect population dynamics near local bifurcation of the resident equilibrium.

We present cases with qualitatively preserved eco-dynamics and also cases with expected irreversible regime transitions. We also present an example of a system, when adaptive dynamics induce hysteresis and periodic regime shifts. The presented results are in agreement with Dercole et al. (2002) and Muratori and Rinaldi (1991). More complex dynamics may occur (see Dercole et al., 2010; Wilsenach et al., 2017 or Dercole and Rinaldi, 2010).

2. Adaptive dynamics and slow-fast eco-evolutionary system

We assume the resident population model as the system (1) of the form

$$\dot{n} = \phi(n, a),$$

where $n = (n_1, \cdots, n_N)$ is a population density vector for an arbitrary number N of species (the species are characterized by an index $i = 1, \cdots, N$) and $a = (a_1, \cdots, a_m)$ is a vector of parameters. The change in the population size or density is described by function $\phi: \mathbb{R}^{N+m} \to \mathbb{R}^N$, that is a smooth enough function dependent on parameters such as the birth and the death rates of the species, carrying capacities and various parameters of functional responses. The parameters $a = a(x)$ of the system (1) are functions of the resident trait value $x = x_r$. We assume that system (1) dynamics is fast, so the resident population settles in a dynamical equilibrium $n^* = n^*(x)$.

Mutations are assumed to be sufficiently rare, but once a mutant has entered the population, it may grow or go extinct according to the invasion exponent (fitness) of mutants in the resident population. The