

Original Research Article

Alternative attractors in an ecological-genetic model of populations with non-overlapping generations

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ABSTRACT

This study classifies and analyzes various bifurcations of fixed points of the simple model of population dynamics with its number described by Ricker's model and intrapopulation parameters determined by a single di-allelic locus. The model considered shows such nonlinear phenomena as multistability and coexistence of alternative attractors, which can violate the simple combination of the action of evolutionary-genetic and density-dependent ecological-dynamic processes, where gene elimination is determined by the genotypes' resource parameters and the population number stability depends on their Malthusian parameters. The most interesting pattern in this regard is existence of polymorphic attractors, when the resource parameter of heterozygotes is not maximal. It presents a clear violation of the principle of natural selection optimality, which is caused precisely by the multistable phenomena of nonlinear dynamics. By which of the alternative attractors the dynamics is characterized by depends sensitively on the initial conditions, even small external influences can become significant, as they can shift the system from one attraction basin to another, and thus fundamentally change the dynamic mode and nature of the evolutionary process.

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1. Introduction

An ecological-genetic approach of modeling that considers connected changes in the genetic structure and population size, was formed due to dynamic development of ideas about density- and frequency-dependent components in the process of natural selection (Birch, 1955; Charlesworth, 1971). Numerous studies in this area gave a picture of the impact of evolutionary factors, first of all the natural selection, on genetic structure changes with population dynamics changes to follow. Those populations face a natural limitation of vital resources, i.e. they are affected by their environmental constraints (MacArthur and Wilson, 1967; Pianka, 1978; Hanski, 1999 etc.).

Even the simplest models of limited population dynamics based on classical mathematical-biological equations (e.g., Verhulst's, Ricker's, Hassell's), which do not take into account genetic factors, exhibit surprisingly complex dynamics (Shapiro, 1972; May, 1975;

Syta and Litak, 2008; Sacker and von Bremen, 2010; etc.). In addition, another nonlinear dynamics effect has recently attracted many investigations (Bezruchko et al., 2002; Berezovskaya et al., 2005; Pimenov et al., 2015; Frisman et al., 2016, etc.). This effect is known as multistability, which is expressed in the simultaneous co-existence of alternative attractors. This phenomenon explains several cases of change in dynamic regimes observed in actual biological populations (e.g., Kausrud et al., 2008; Pawlowski and Cabezas, 2008; Kilgo et al., 2010, 2012; White, 2011); and it has great importance in exploited populations (e.g., Auger et al., 2010; Jackson and Ditchkoff, 2013; McCoy et al., 2013; Costa et al., 2016).

Ecological-genetic models are naturally multistable because they commonly possess several genetically different fixed points and transition to these points dependent on the initial conditions. At that, evolutionary dynamics does not simply determine ecological dynamics as one might think. In contrast, the direction of evolution is not only influenced by the genotypic fitness but might even depend on local population densities. Therefore, the investigation of multistability areas in ecological-genetic models appears beneficial.

The present study is devoted to a variety of possible dynamic regimes and investigates multistability regions in the uniform population model, where the dynamics is described by Ricker's

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model and the values of its intrapopulation parameters are genetically defined (Zhdanova and Frisman, 2005).

2. The model

We consider a generalization of Ricker’s model (Ricker, 1954) by considering the action of natural selection on a single monogenic adaptive trait (Fisher, 1930) as follows:

$$\{x_{n+1} = \bar{w}_n x_n q_{n+1} = q_n (w_{AA} q_n + w_{Aa} (1 - q_n)) / \bar{w}_n, \quad (1)$$

where n is the number of generation; $\bar{w}_n = w_{AA} q_n^2 + 2w_{Aa} q_n (1 - q_n) + w_{aa} (1 - q_n)^2$ is the average fitness of the population in the n th generation; x_n is the population number in the n th generation and is measured in non-dimensional units; q_n is the frequency of allele A in the n th generation; and $w_{AA}(n)$, $w_{Aa}(n)$, and $w_{aa}(n)$ are the fitnesses of genotypes AA , Aa , and aa , respectively, in the n th generation. The genotype fitness exponentially depends on the population size: $w_{ij}(n) = \exp(R_{ij}(1 - x_n/K_{ij}))$. R_{ij} and K_{ij} are the Malthusian and resource parameters of the ij genotype, respectively. Moreover, R_{ij} and K_{ij} characterize the reproductive potential of a genotype and the capacity of the ecological niche, respectively. If the entire population comprises individuals with the ij th genotype, then the equilibrium number is K_{ij} . Note that both parameters are non-negative ($R_{ij} > 0$ and $K_{ij} > 0$), the coefficients R and K are measured in dimensional and non-dimensional units, respectively. The considered type of natural selection is biologically meaningful because numerous laboratory and field studies have demonstrated r - and K -selection strategy (Long and Long, 1974; MacNaughton, 1975; Graham, 1977). The concept of r - K selection considers the struggle for existence as defined by the different strategies of survival at the genetic level. Some genotypic groups rapidly propagate and therefore exhibit a high reproductive potential (r -strategy), whereas other groups adapt to limited resources and present a high capacity of the ecological niche (K -strategy).

The basic assumptions made in constructing model (1) are as follows: genetic variation is controlled by a single diallelic locus (with alleles A and a) and the phenotype of an individual is strongly determined by its genotype, the population is panmictic, the Mendelian inheritance rules are followed. Generations are considered non-overlapping; i.e., the parental generation is eliminated after producing the progeny. This property is possessed by species with a short lifecycle, high fertility, and a single reproduction (annual plants, many insects, and some migratory fishes), the populations are usually of the same age. The next generation almost simultaneously emerges from eggs or seeds,

more or less simultaneously grows up, propagates, and then dies. In these species, the parental generation does not meet their offspring. For example, in all known grasshoppers, overwintering concerns only eggs, which are laid in the ground in egg capsules, while adult insects die out by the winter. A substantially detailed discussion of these limitations and their biological meaning is provided in (Fisher, 1930).

In addition we assume that an equilibrium point of a population number (x^*) exists, where the fitnesses of all genotypes are equal. Thus, $w_{AA}(x^*) = w_{Aa}(x^*) = w_{aa}(x^*)$ (see Fig. 1). This limitation simplifies the current study because the limitation reduces the number of independent parameters of the model. Such limitation also allows the simulation of biologically interesting situations, where different genotypes are advantageous in a large ($x > x^*$) or small ($x < x^*$) population size (see Fig. 1, left). Hence, several genotypes are considerably fecund, whereas others are adapted to resource limitation, what allows to compare r - and K -selection strategies. For example, the Arctic fox (*Alopex lagopus*, family *Canidae*, order *Carnivora*) exhibits such genetically defined difference in an individual reproductive strategy, where both the litter size and different fitnesses of pups in large and small litters in these populations are defined by a single diallelic locus (Axenovich et al., 2007). The properties of the trait considered fit well into the r - K -selection model as genotypes producing more offsprings, i.e. with a larger reproductive potential (R_{ij}), are less fitted to limited food resources, which are described by their parameters K_{ij} , than the genotype with a lower reproductive potential (R_{aa}). Indeed under the same conditions (with similar food availability restrictions), as the biological investigations of arctic foxes revealed (Tannerfeldt and Angerbjörn, 1998a,b; Elmhagen et al., 2000), small litters show higher survival. Thus, by the end of their breast-feeding they have more pups survived than the others, initially larger litters.

Thus, model (1) has five independent parameters (i.e., K_{AA} , K_{Aa} , K_{aa} , R_{AA} , and R_{Aa}), and R_{aa} may be calculated using the following formula (see Appendix A for more details):

$$R_{aa} = \frac{\ln w_{AA}(x^*)}{1 - x^*/K_{aa}}, \quad x^* = \frac{R_{Aa} - R_{AA}}{R_{Aa}/K_{Aa} - R_{AA}/K_{AA}}. \quad (2)$$

From (2), one can conclude that $x^* > 0$, as shown in (Fig. 1 (left) when $\{K_{AA} < K_{Aa}, R_{AA} > R_{Aa}\}$ and in a symmetrical one, when $\{K_{AA} > K_{Aa}, R_{AA} < R_{Aa}\}$; providing that, $R_{ij} > 0$ and $K_{ij} > 0$.

For the case in Fig. 1 (right), the values of x^* are positive if the following conditions hold:

$$\{R_{Aa}/K_{Aa} > R_{AA}/K_{AA}, \text{ when } R_{Aa} > R_{AA}\}, \\ \{R_{Aa}/K_{Aa} < R_{AA}/K_{AA}, \text{ when } R_{Aa} < R_{AA}\}.$$

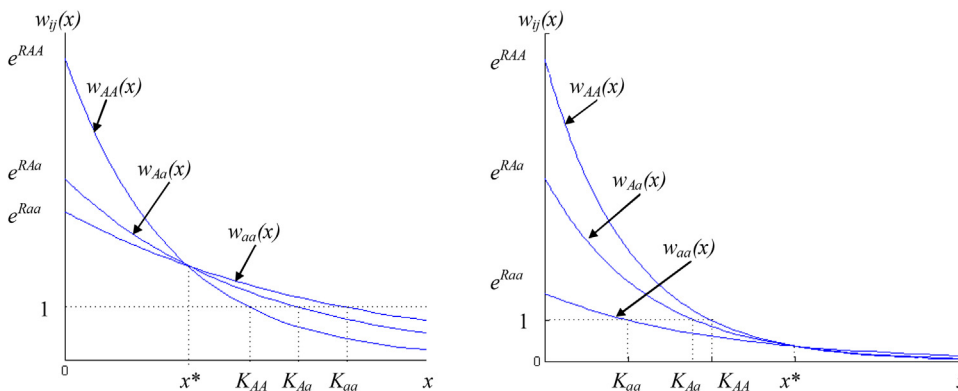


Fig. 1. Examples of the dependence of the genotypic fitnesses (w_{ij}) from population size (x), provided that an equilibrium point of a population size (x^*) exists, where fitnesses of all genotypes are equal. (Left) $x^* < \min(K_{ij})$. (Right) $x^* > \max(K_{ij})$.

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