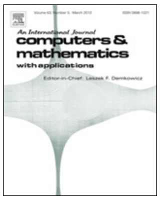
Computers and Mathematics with Applications 69 (2015) 145–156

Contents lists available at ScienceDirect

Computers and Mathematics with Applications

journal homepage: www.elsevier.com/locate/camwa



On a singular perturbation problem arising in the theory of Evolutionary Distributions

Yosef Cohen [a], Gonzalo Galiano [b,*]

[a] Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, 1980 Folwell Avenue, St. Paul, MN 55108, USA
[b] Department of Mathematics, Universidad de Oviedo, c/ Calvo Sotelo, 33007-Oviedo, Spain

ARTICLE INFO

Article history:
Received 3 January 2014
Received in revised form 30 September 2014
Accepted 4 November 2014
Available online 30 December 2014

Keywords:
Evolutionary Distributions
Singular perturbation
System of partial differential equations
Existence of solutions
Numerical simulations

ABSTRACT

Evolution by Natural Selection is a process by which progeny inherit some properties from their progenitors with small variation. These properties are subject to Natural Selection and are called adaptive traits and carriers of the latter are called phenotypes. The distribution of the density of phenotypes in a population is called Evolutionary Distributions (ED). We analyze mathematical models of the dynamics of a system of ED. Such systems are anisotropic in that diffusion of phenotypes in each population (equation) remains positive in the directions of their own adaptive space and vanishes in the directions of the other's adaptive space. We prove that solutions to such systems exist in a sense weaker than the usual. We develop an algorithm for numerical solutions of such systems. Finally, we conduct numerical experiments—with a model in which populations compete—that allow us to observe salient attributes of a specific system of ED.

1. Introduction

Evolution by Natural Selection [1], can be distilled to three principles: (i) inheritance with (ii) variation (mutations) and (iii) natural selection. Phenotypes are traditionally defined as organisms that display some traits. Traits may be identified with color of skin, height, speed of running, length of a molecule of protein, volume of cells and so on. We use a restricted definition of phenotypes, namely an organism that displays some trait that is subject to natural selection. With abuse of the English language, we call these *adaptive traits*. For example, an adaptive trait of Polar bears may be the thickness of hair in their fur, where length of hair is presumably inherited.

Now consider the speed of running of prey to be an adaptive trait. Assume that different values of speed are inherited with some variation and are subject to natural selection. Three issues of interest emerge. First, a value of a trait is an attribute of an organism. Second, some variation in these values is not "recognized" as such by natural selection. In our example of speed of running, selection influences survival of those prey that run at, say, 20 km/h and those that run at 22 km/h equally. This may be so, even when these two different speeds are inherited. Ergo, a value of an adaptive trait is in fact a set of values. This set identifies a subpopulation made of organisms that belong to a single phenotype where the population is made of phenotypes that carry all values of the adaptive trait. We shall get to the third issue in a moment.

Mathematical models of evolution may be cast via differential equations that are either deterministic or stochastic. Starting with individual-based models, also referred to as particle models, is useful since one can construct such models based on first principles. In such models, particles may represent single organisms that may be classified as phenotypes—they exhibit particular values of adaptive traits. Particles may also represent a subpopulation of phenotypes; namely a set

---

[*] Corresponding author. Tel.: +34 985103343; fax: +34 985103354.
E-mail addresses: yc@umn.edu (Y. Cohen), galiano@uniovi.es (G. Galiano).

http://dx.doi.org/10.1016/j.camwa.2014.11.003
0898-1221/

of phenotypes that are lumped into a single subpopulation – of population of all phenotypes – based on the granularity of natural selection. Granularity refers to the idea that in acting upon phenotypes, certain range of values of adaptive traits are indistinguishable by natural selection. This range defines a subpopulation of phenotypes which in fact represents the unit of natural selection.

In modeling evolution by natural selection, one often wishes to switch from an individual-based to a PDE-based approach. A typical procedure consists in considering first the dynamics for single individuals. Then, by letting the number of individuals, N, increase to infinity, one may determine the evolution laws for the population density.

In a nutshell, one begins with a definition of some property that is represented by a particle. In our case, such property consists of values of an adaptive trait.

Then, based on first principles, a Lagrangian description for a system of N particles is deduced. In particular, laws for the evolution of the counting process describing particle spatial frequency are obtained.

In order to pass to a continuum Eulerian description, one first considers a rescaled counting process, typically the relative frequency of traits, and then study the limit $N \to \infty$ of the Lagrangian description. In this passing to the limit two mathematical problems arise.

The first problem, not addressed in this article, is showing the convergence of the sequence of discrete measures (relative frequencies) to a continuous limit measure (density) which may be determined as a solution of a PDE problem. We refer the reader to [2–4] for results on adaptive evolution of a single population. Similar mathematical problems have been studied in spatial dynamics of population [5–9], in the theory of chemotaxis and phototaxis [10,11], or in flow in porous medium [12,13].

The second problem is proving that the limiting evolution PDE, along with appropriate boundary conditions and initial data, is a well-posed problem. Furthermore, that the solution to the problem inherits the essential properties – such as positiveness and boundedness – of the discrete measures.

While in the case of a single population the limit PDE is uniformly parabolic, and thus the standard theory of existence and uniqueness of solutions applies, in the case of a multipopulation model the resulting system of PDEs has a peculiar degenerated parabolic structure.

To understand the lack of uniform parabolicity of the system observe that selection affects the dynamics of coevolving populations through mortality, in which all the populations are involved—and therefore their so-called adaptive trait spaces too. However, the only cause of diffusion is mutation, which occur only in each population adaptive space. Thus, the resulting PDE system is a special case of anisotropic diffusion in which diffusion of each population remains positive in the directions of their own adaptive space but vanishes in the directions of the other's adaptive spaces.

The main aim of this article is to find conditions on the data problem under which the existence of solutions of the multipopulation model may be guaranteed. Chipot and coworkers studied related issues in the framework of the theory of singular perturbation. In [14] they proved existence of solutions for a general class of time-independent boundary value problems. They also proved existence and some additional properties of solutions for a particular case of a nonlocal evolution boundary value problem. The problems they studied addressed a single equation; we address a system of equations. Yet, we fundamentally rely on their work.

The complexity of the dynamics of evolution implies that exact solutions to the problem in terms of elementary functions are not available. Even analytical qualitative properties of solution are hard to obtain. Thus, in Section 4, we introduce a numerical discretization of the problem under the Finite Element Method framework. Then, we construct some numerical experiments to observe salient features of the system of ED that cannot be observed otherwise. We also use the numerical experiments to draw conclusions about potential dynamics of evolution under such peculiar systems. See [15–18] for related numerical approaches.

2. Mathematical model

In this section we present a brief and heuristic derivation of the mathematical model we study in the rest of the paper. A rigorous deduction of the single population case may be found in [2].

Consider a population in which individuals give birth and die at rates that are determined by values of an adaptive trait, **x**, that they exhibit (a so-called phenotype) and by interactions with other phenotypes. The population is characterized at any time t by the finite counting measure

$$\nu_t = \sum_{j=1}^{N(t)} \delta_{\mathbf{x}_t^j}$$

where $\delta_{\mathbf{x}}$ is the Dirac measure at **x**. The measure ν_t describes the distribution of phenotypes over the trait space at time $t \in [0, T]$. Here, $T > 0$ denotes a final time arbitrarily fixed, $N(t)$ is the total number of phenotypes alive at time t, and $\mathbf{x}_t^1, \dots, \mathbf{x}_t^{N(t)}$ denote the values of an adaptive trait—which we identify with individuals (or particles).

Let K be the initial number of individuals and define a normalized population stochastic process by

$$X_t^K = \frac{1}{K}\nu_t^K.$$