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Paradox of enrichment: A fractional differential approach with memory

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HIGHLIGHTS

- We formulate the fractional counterpart of the Rosenzweig model.
- We analyze the stability of this fractional order model.
- We identify a threshold for the memory effect parameter.
- Below this threshold value the system is always stable independent of enrichment.
- Fractional differential equations may be an important tool for resolving the paradox of enrichment.

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ABSTRACT

The paradox of enrichment (PoE) proposed by Rosenzweig [M. Rosenzweig, The paradox of enrichment, Science 171 (1971) 385–387] is still a fundamental problem in ecology. Most of the solutions have been proposed at an individual species level of organization and solutions at community level are lacking. Knowledge of how learning and memory modify behavioral responses to species is a key factor in making a crucial link between species and community levels. PoE resolution via these two organizational levels can be interpreted as a microscopic- and macroscopic-level solution. Fractional derivatives provide an excellent tool for describing this memory and the hereditary properties of various materials and processes. The derivatives can be physically interpreted via two time scales that are considered simultaneously: the ideal, equably flowing homogeneous local time, and the cosmic (inhomogeneous) non-local time. Several mechanisms and theories have been proposed to resolve the PoE problem, but a universally accepted theory is still lacking because most studies have focused on local effects and ignored non-local effects, which capture memory. Here we formulate the fractional counterpart of the Rosenzweig model and analyze the stability behavior of a system. We conclude that there is a threshold for the memory effect parameter beyond which the Rosenzweig model is stable and may be used as a potential agent to resolve PoE from a new perspective via fractional differential equations.

1. Introduction

The paradox of enrichment (PoE) phenomenon in population ecology was first proposed by Michael Rosenzweig in 1971 [1]. Rosenzweig observed that enrichment may destroy the steady state of a predator–prey system. He formulated his model using ordinary differential equations (ODEs) and considered enrichment by increasing the prey-carrying capacity.

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He observed that this gradually leads to destabilization of the system, usually into a limit cycle. This cyclical pattern was further studied by May [2] and Gilpin and Rosenzweig [3]. Enrichment leads to destabilization of the equilibrium of the Rosenzweig and many other models [4]; huge amplitudes occur that frequently drive population densities to very low values and this may result in extinction. The word ''paradox'' is used because enrichment leads to extinction. Since the 1990s, the word ''paradox'' has also been associated with the fact that destabilization is not always (or rarely) observed in natural environments, as discussed by Jensen and Ginzburg [5]. They reviewed the literature on experimental attempts to demonstrate PoE and found an insufficient number of studies in favor of PoE. Some commonly misinterpreted examples and experiments (artificial lake eutrophication, *Didinium–Paramecium* systems [6,7], Rotifer–Algae systems [8]) addressing the question of whether PoE exists need further discussion.

Several theoretical and empirical studies have been carried out in attempts to explain the PoE phenomenon. Roy and Chattopadhyay provide a detailed review of the studies and a brief overview of the proposed solutions [4]. They described some reasonable mechanisms, such as the presence of inedible prey, invulnerable prey, unpalatable prey, ratio-dependent functional responses, spatiotemporal chaos, inducible defense, density-dependent predator mortality and toxic food, to resolve the paradoxical outcome of ecosystem enrichment. Several additional mechanisms have also been proposed. For example, Abrams and Roth proposed refuges and immigration as a possible solution [9]. More recently, Mougi and Nishimura showed that rapid trait evolution of predator–prey species can stabilize the system [10]. An imperfect optimal foraging mechanism was proposed by Mougi and Nishimura [11]. Rall et al. predicted that a sigmoidal or predator inference functional response can dampen population oscillations due to enrichment that resolves PoE [12]. Disease in ecological systems has been recognized as an essential mechanism in different ecological issues. Sharp and Pastor recently considered a density-dependent susceptible deer population, an infected population and an environmental pool of prions that infect the deer population [13]. They showed that the disease population has the ability to dampen population oscillations. Solutions to the PoE problem have been established by several authors from diverse perspectives and dimensions, but most of the solutions have some common factors associated with the behavioral aspects of predator–prey species at the individual level and inducible or morphological defense mechanisms of the prey. However, solutions that consider community-level organization are still lacking. Knowledge of how learning and memory modify behavioral responses to species is a key factor in making a crucial link between the species and community levels [14]. Resolution of PoE via these two organizational levels can be interpreted as a microscopic- and macroscopic-level solution.

In statistical physics the connection between microscopic dynamics in a stochastic system and a macroscopic description of their behavior as a whole is very attractive [15]. It has been already established that the macroscopic behavior of stochastic systems contains a manifestation of microscopic dynamics due to memory effects [15].

Memory in the biological domain in physical systems is manifest as a series of events that induce episodic memory [16,17] containing information about past and present events and can help in making future decisions [18]. Biological systems are also enriched with ecological memory [19]. Memory relates to historic events and requires an entire long-term record for analysis. For example, seasonal succession of phytoplankton in lakes responds to small changes in trophic structure and natural fluctuations of gradients [19]. Aquatic and phytoplankton systems possess a remarkable memory of climatic events [20]. Apart from such climatic phenomena, aquatic zooplankton exhibit memory-based phenomenological responses: small changes in the environment induce morphological defense organs such as helmet formation and the development of spines through cyclomorphosis [21]. These changes are due to a mixed seasonal and genetically inherited reaction [22] induced over long time scales, suggesting a phenotypic change through memory-based actions. Prey refuge, group hunting and prey swarming are all well-coordinated actions based on memories of past events that lead to cultural learning [14]. Experience accrued through learning may direct anti-predator responses [23–25]. In aquatic systems, learning of chemical cues and the production of counter responses are well documented among zooplankton [26–31]. Westerlund remarked that, surprisingly, even ''dead matter has memory'' [32]. A recent study by Zheng et al. [33] revealed that discrete earthquake events are related to seismic memory.

Fractional derivatives provide an excellent tool for describing memory and the hereditary properties of various materials and processes [34,35]. In other words, fractional dynamic systems in applications can adequately represent some long-term memory and non-local effects that are typical for many anomalous processes [36]. In this calculus, a Caputo derivative implies a memory effect via convolution between an integer-order derivative and a power of time [37]. Note that a fractional-order system is more stable than its integer counterpart since the stability domain in the complex space of eigenvalues of the linearized system for fractional differential equations (FDEs) remains contained and is larger than the corresponding domain for ordinary differential equations [38]. FDEs also help in reducing errors arising from neglected parameters in modeling of real-life phenomena [39].

Ahmed and Elgazzar used FDEs to study non-local epidemics synergistic with other complex adaptive systems such as severe acute respiratory syndrome, avian flu, and foot-and-mouth disease [40]. Local and non-local interactions were widely observed in recent outbreaks of the above diseases and the model proposed by Ahmed and Elgazzar captured these interactions. Arafa et al. also used FDEs to elegantly model childhood diseases with constant vaccination and obtained an approximate analytic solution through the homotopy analysis method [41]. Immune systems include both antigen-specific and systematic response and involve memory. A fractional-order example of two immune effectors attacking an antigen was proposed by Hashish and Ahmed [42]. Apart from ecology and epidemiology, FDEs have interdisciplinary applications in various fields. For example, nonlinear earthquake oscillations can be modeled using fractional derivatives [41] and a fluid-dynamics traffic model with fractional derivatives can eliminate the efficiency arising from assumption of continuous traffic