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Q1 A multiple phenotype predator–prey model with mutation

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HIGHLIGHTS

- Mutation is modelled via a coupled map lattice.
- Results are presented for Ricker and logistic models for the prey dynamics.
- Predator mutation enhances predator survival for a range of predation rates.
- The most dominant predator is the one that has the most focused predation strategy.

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ABSTRACT

An existing multiple phenotype predator–prey model is expanded to include mutation amongst the predator phenotypes. Two unimodal maps are used for the underlying dynamics of the prey. A predation strategy is also defined which differs for each of the predators in the model. Results show that the introduction of predator mutation enhances predator survival both in terms of the number of phenotypes and total population for a range of values of the predation rate. In general, the dominant predator phenotype is the one which is most focused on the prey phenotype with the largest population.

1. Introduction

The mathematical modelling of predator–prey population dynamics goes back to the work of Lotka [1] and Volterra [2] and their independent discovery of the pair of coupled non-linear differential equations which now bears their names [3]. Since this work predator–prey systems have been modelled via a wide range of mathematical and computational techniques, including the use of discrete time population models, spatial models, and individual agent based models, with the sophistication of the modelling increasing with the rise in computer power.

In the field of ecological modelling significant research has focused on two species predator–prey models, which have been used to investigate chaotic population dynamics [4–8], the effect of the prey growth rate [9] and spatial dispersal [10–12]. Two species models have been generalised to multiple predator–prey systems, including the study of resulting chaotic behaviour, and the effect of implementing various functional responses (the effect of predation, per predator, upon the prey species) upon the dynamics [13–16]. However, in general less work has been undertaken looking at multiple species predator–prey models where the system has been expanded to allow for multiple competing predators and prey.

The modelling of functional response is one of the most studied aspects of mathematical ecology, with Holling's Type II disc equation [17] proving particularly popular. Several sophisticated forms have been proposed, and their relative ecological merits have been debated [18]. Other studies have suggested that models featuring nonlinear functional responses

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and adaptive foraging may be essential for the maintenance of stable, complex ecosystems [19]. The relationship between complexity and stability [20] has remained a significant issue within theoretical ecology since May's (1973) [21] work on random graphs challenged the intuitive belief that greater complexity increases the stability of an ecosystem. The issue has been explored in some detail using both models and empirical data. Various definitions of stability [22] have been investigated in the context of ecological networks in which predator–prey ratios, the proportion of possible feeding links in the network [23], the effects of competition between species, and the proportion of weak feeding links [24] are varied.

A key area of the study presented in this paper is the inclusion of mutation in a predator–prey ecosystem. Mutation has previously been introduced into both single species predator–prey ecosystems [25,26] where it was used to simulate adaption towards the environment, and in multiple species predator–prey models [27] where the various traits of the predator and prey are allowed to evolve, introducing new phenotypes into the ecosystem. Several eco-evolutionary models have been developed that combine random mutation and resulting natural selection within population dynamics models [28–33]. A key feature of these models is that the species themselves are not pre-selected, and the trophic relationships that are present in the resulting food web are an emergent result of the selection process operating on population dynamics. An overview of the development of one such model in the light of historical food web research can be found in Ref. [34].

A further approach is to allow populations to occupy a spatially extended region, thus producing a predator–prey system that models the dynamics of the species in both space and time. Such models have been developed in continuous space and time, via reaction–diffusion based predator–prey models [35,36], and in discrete space and time via coupled map lattice (CML) based models [37–39], with the latter being the approach taken in the current paper. Studies in the physics literature have considered the dynamics on such models [40,41], and they have been applied to modelling population dynamics on spatial systems of plants [42] and insects [43]. Multiple-species predator–prey relationships on a lattice are studied using the discrete generalised Lotka–Volterra equations in Ref. [44]. Using a lattice has the advantage of being relatively simple to compute, whilst also allowing simple modelling of neighbouring ecological environments to be modelled. How these ideas are implemented in the present study will be discussed in more detail later.

This paper uses a generalised multiple phenotype form of a discrete time predator–prey model proposed by Neubert and Kot [4] that has been previously studied by Mullan et al. [45]. Here it is further expanded to allow mutation amongst the various predator and prey phenotypes that occupy the ecosystem, forming a mutating predator–prey model with much heterogeneity. A variation of the model studied here where a single predator predates upon a set of mutating prey has been studied by Mullan et al. [46].

The work presented here expands on [46] to consider mutation for both the predators and the prey. Results from a 10 predator–10 prey ecosystem, both with and without mutating predators are discussed, first showing a broad overview of where survival occurs in the model based on the assigned control parameters, and then with a focus being placed on the underlying dynamic behaviour of the phenotypes within the model as its configuration changes. Both the Ricker model and logistic map are used to model the prey dynamics with comparisons being drawn between the two unimodal maps.

2. Multiple phenotype predator–prey model

In Ref. [46] a multiple phenotype model based on work by Neubert and Kot [4] was defined as

$$N^{(j)}_{t+1} = \exp\left(-\left(\sum_{i=1}^{m}(f^{(ij)}c_{ij})P^{(i)}_{t}\right)\right)N^{(j)}_{t}\exp\left(r_j\left(1-N^{(j)}_{t}\right)\right) \tag{1a}$$

$$P^{(i)}_{t+1} = \sum_{j=1}^{n}(f^{(ij)}c_{ij})N^{(j)}_{t}P^{(i)}_{t} \tag{1b}$$

where $N^{(j)}_t$ represents the population density of the jth prey phenotype at time step t and $P^{(i)}_t$ represents the ith predator phenotype at time step t, with c_{ij} and r_j acting as the control parameters. The two generalised equations allow for m predators and n prey to occupy the ecosystem, with each prey having an individual r value corresponding to its growth rate, and a c_{ij} term, which measures the predatorial effectiveness of the ith predator at predating upon the jth prey. The term $f^{(ij)}$ models how predator i divides its effort hunting the jth prey phenotype.

Here the model is further expanded with the introduction of mutation amongst the predators and prey. This has been achieved by introducing CML based mutation. A variation of (1) which utilises the Ricker model to govern the dynamics of the prey is as follows:

$$N^{(j)}_{t+1} = \sum_{k=1}^{n}p^{prey}_{kj}\exp\left(-\left(\sum_{i=1}^{m}(f^{(ik)}c_{ik})P^{(i)}_{t}\right)\right)N^{(k)}_{t}\exp\left(r_k\left(1-N^{(k)}_{t}\right)\right) \tag{2a}$$

$$P^{(i)}_{t+1} = \sum_{k=1}^{m}p^{pred}_{kj}P^{(k)}_{t}\sum_{j=1}^{n}f^{(kj)}\max(0, c_jN^{(j)}_{t}-P^{(k)}_{t}) \tag{2b}$$

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