Red Queen dynamics in a predator-prey ecosystem

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1. INTRODUCTION

Coevolution between predators and prey can lead to situations in which neither antagonist improves its fitness, since both populations continually co-adapt to each other. Here, we take an eco-evolutionary approach to this 'red queen' phenomenon (van Valen, 1973) to explain it as an interaction between population dynamics and evolutionary dynamics.

2. METHODS

We use models of predator-prey coevolution based on (van der Laan & Hogeweg, 1995) and (Savill & Hogeweg, 1997): an individual-based simulation model and its mean-field approximation (ODE model). The simulation model shows complex population dynamics and evolutionary red queen dynamics. These results are interpreted analytically in terms of the ODE model.

2.1 Simulation

We use a spatially explicit individual-based model, implemented in Framsticks (Komosinski, 2003). This model simulates an environment which is inhabited by a population of prey and a population of predators.

Individuals and interaction.
Prey are static plant-like entities that reproduce periodically (logistically) and can be consumed by predators. Predators are modelled as situated agents that perform chemotaxic behavior towards prey. Predators loose energy every time step, and can gain energy by predation. A predator reproduces when its energy exceeds a certain threshold. Predation (or consumption) of a prey by a predator is handled by transferring the energy of the prey to the predator, which causes the prey to die. Whether an encounter between a prey and predator results in predation (i.e. energy transfer) depends on the phenotypes of both individuals.

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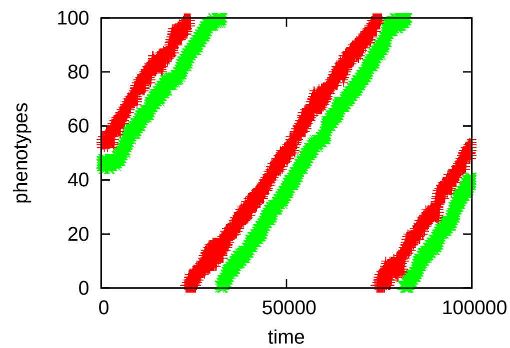

Figure 1: Phenotypes and phenotypic distance over time. Prey (in green) escapes from predators (in red) and predators chases prey through phenotype space. Red line shows the population-average phenotypic difference over time.

Phenotypes.
The probability of predation is maximal if both have the same phenotype, but decreases with the difference between phenotypes according to a Gaussian probability distribution. All individuals are specified with an inheritable phenotype. Phenotypes are natural values along a wrapped-around phenotype space [0,100]. The minimal phenotypic difference is used to determine the probability of predation.
Offspring have a small probability of mutation, which is equal for prey and predators. The mutation is implemented as a shift by one unit ($mutant = parent \pm 1$).

3. RESULTS

Simulations show longterm ecological coexistence of predators and prey, due to a continuous evolutionary arms race.

Population sizes are relatively small (<250) and therefore subject to stochasticy. They nevertheless show regular oscillatory behavior, before settling in a relatively stable region of attraction (at approx. 200 prey $\pm$50, 125 predators $\pm$25, results not shown). After 75000 timesteps, the system returns to oscillatory behavior, but soon recovers stability. Predators and prey coexist indefinitely (neither goes extinct).

Evolutionary dynamics.

The evolution of phenotypes, plotted in figure 1, shows an evolutionary arms race through (wrapped) phenotype space. After an initial increase, the phenotypic difference (red line) remains relatively stable at values $(12 - 15)$. A temporary decrease is observed after 75000 timesteps, coinciding with a population dynamical change.
The evolutionary dynamics seem to be constrained to a region in which coexistence (hence coevolution) is possible.

4. THEORETICAL ANALYSIS

To understand these constraints, we construct an analytical ODE model of the population dynamics, and relate the evolutionary dynamics to the change of a parameter in this model. A formal concept of fitness is also derived.

Ecological model.

The mean-field approximation of the simulated ecological interactions turns out to be equivalent to a well-studied model described by Beddington (1975):

$$\frac{dR}{dt} = rR(1 - \frac{R}{K}) - \frac{aRC}{h + R + eC}$$
$$\frac{dC}{dt} = \frac{caRC}{h + R + eC} - dC \quad (1)$$

where R (resources) is used to denote prey density and C (consumers) is used for predators. Further, r is intrinsic growth rate, K is prey carrying capacity, a is maximum predation rate, h represents handling time, c is biomass conversion rate, e is predator interference, and d is the predator death rate.

Evolutionary dynamics.

In this ecological model, evolution can be understood simply as changes of the model parameters. In this case, we focus on changes of the maximum predation rate a, which is proportional to the phenotypic difference between predator and prey (determining the predation probability). Predation rates are low for individuals or populations that are phenotypically very different, and high for those that are similar. As the predation rate a increases above a certain critical value, a qualitative change occurs, as the system moves from a region of stable steady states (fixed point attractors) to unstable equilibria (causing oscillations). Such occurred after 75000 time steps.

Fitness.

A formal concept of predator fitness helps us to understand this qualitative change and the constraints, and is obtained from the model above: $R_0 = (caR/(h + R + eC))/d$.

Figure 2 plots the fitness against the phenotypic difference. In ideal situations for predators (e.g. maximum prey density, no predator interference), the Gaussian distribution is recovered (top line). When ecological interactions are taken into account, however, the fitness distribution shows a bifurcation, left of which predators can obtain many different fitness values as they are subject to population dynamical oscillations. High predator fitness induces an increased selection pressure on the prey population, that subsequently evolves away. At high phenotypic differences, predator fitness R_0 drops below 1 which results in (partial) extinction

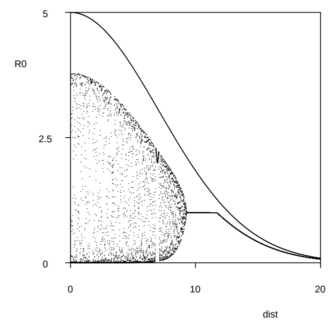

Figure 2: Ideal fitness (top line) and ecologically-embedded fitness (below) as a function of phenotypic distance

of the predator population, causing a selective pressure towards 'chasing' prey phenotypes. The predator population is stable in the flat region of phenotypic differences values, where fitness $R_0 = 1$. The ecological constraints on both sides (low and high difference) cause the coevolving populations to remain in a domain in phenotype space in which coexistence of predators and prey is possible.

5. CONCLUSIONS

A simulation model and its analytical ODE model are presented to show and explain the emergence of red queen dynamics as an interaction between population dynamics and evolutionary dynamics. Evolution of phenotypes (and phenotypic difference) causes (qualitative) changes in population dynamics. These population dynamical, reversely, constrain the evolutionary dynamics to a region of coexistence. This eco-evolutionary interaction causes red queen dynamics by enabling a sustained coexistence of coevolving predators and prey, without either side gaining fitness benefits over the other.

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