

# Fitness in fluctuating environments

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**Short Abstract** — Using a simple population dynamics model we show that the relative fitness of two phenotypes competing in a dynamical environment depends not only on the static averages but also on the time scales and temporal correlation of environmental conditions.

**Keywords** — dynamic environment, evolution, competition.

## I. INTRODUCTION

ORGANISMS react to long-term changes in environmental conditions by sequential fixation of new genome sequences corresponding to increasingly more adapted phenotypes. However, often environmental changes are faster than the characteristic time for mutation-selection cycles needed to evolve an optimal phenotype. In such cases, depending on the structure and time scales of the fluctuations, a dynamic environment promotes sensing [1], modularity [2] and can change the speed of adaptation [3,4]. In addition, dynamic environments can generate new dynamic (fluctuating) fitness landscapes.

The relevant parameters describing the evolutionary response of a population to a changing environment are the rate at which new genotypes are created (mutation rate), the relative fitness of new phenotypes and the total population size. We concentrate on the case of environments oscillating faster than an individual's lifetimes but slower than the typical time of fixating a new mutation. In this parameter region, the fluctuating birth and death rates of individuals can still be coarse-grained into effective constant population sizes and selection coefficients, which are non-trivial. This situation is relevant for bacterial populations confronted with daily environmental changes (natural or artificial) [5] of for longer living organism affected by seasonal variations.

## II. MODEL

We describe dynamics of a mutant phenotype,  $x_2$ , competing with the wild type,  $x_1$ , according to the Lotka-Volterra model [6]

$$\begin{aligned}\frac{dx_1}{dt} &= [b_1(t) - d_1(t)(x_1 + x_2)]x_1, \\ \frac{dx_2}{dt} &= [b_2(t) - d_2(t)(x_1 + x_2)]x_2.\end{aligned}$$

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Here  $b_i$  and  $d_i$  are the birth and the death parameters, respectively, and a non-linear coupling of the two populations models competition for resources. The environmental fluctuations are modeled by using time dependent, periodic, off-phase birth and death parameters.

## III. RESULTS AND CONCLUSIONS

In the limit of small differences between the two populations' parameters, the fixation dynamics is governed by a single effective parameter, describing the relative growth rate difference of the two populations. In the limit of infinitely slow environmental changes (but faster than the fixation dynamics) this fitness difference can be expressed as a function of,  $b_i$  and  $d_i$  averaged over all of the environmental states and independent of the period of the fluctuations. Due to the non-linear dependence of the growth rates on the parameters, the average fitness difference is not the same as the fitness difference for the average environment.

This quasi-steady state approximation breaks down for faster environmental changes. The speed of adaptation is now dependent not only of the period of environmental changes but also on the particular sequence of successive environmental states. In particular the first non-adiabatic correction is always anti-symmetric with respect to time reversals. As long as the fluctuations in the parameters are large, this non-adiabatic correction is of the same order of magnitude in the birth and death variation as the quasi-steady state contribution to the fitness difference.

We conclude that the species with the fitness advantage in the average environment, with the average fitness advantage over all environments, and with the average fitness advantage for a particular time course of the environment are not necessarily the same species. In particular, a naively deleterious mutation can fixate in a population due to these temporal effects. We believe this to hold true independently of many of the simplifying assumptions of our toy model.

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