

Learning Dynamics and the Co-Evolution of Competing Sexual Species*

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Abstract

We analyze a stylized model of co-evolution between any two purely competing species (e.g., host and parasite), both sexually reproducing. Similarly to a recent model of Livnat *et al.* [11] the fitness of an individual depends on whether the truth assignments on n variables that reproduce through recombination satisfy a particular Boolean function. Whereas in the original model a satisfying assignment always confers a small evolutionary advantage, in our model the two species are in an evolutionary race with the parasite enjoying the advantage if the value of its Boolean function matches its host, and the host wishing to mismatch its parasite. Surprisingly, this model makes a simple and robust behavioral prediction. The typical system behavior is *periodic*. These cycles stay bounded away from the boundary and thus, *learning-dynamics competition between sexual species can provide an explanation for genetic diversity*. This explanation is due solely to the natural selection process. No mutations, environmental changes, etc., need be invoked.

The game played at the gene level may have many Nash equilibria with widely diverse fitness levels. Nevertheless, sexual evolution leads to gene coordination that implements an optimal strategy, i.e., an optimal population mixture, at the species level. Namely, the play of the many “selfish genes” implements a time-averaged correlated equilibrium where the average fitness of each species is exactly equal to its value in the two species zero-sum competition.

Our analysis combines tools from game theory, dynamical systems and Boolean functions to establish a novel class of conservative dynamical systems.

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An exciting recent line of work in the theory of computation has focused on the algorithmic power of the evolutionary process (Valiant [22], Livnat *et al.* [11, 10]). The latter two papers identified as interesting the case of a sexually reproducing, haploidal, and panmictic species, evolving in a fixed environment according to variants of Multiplicative Weights Update

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dynamics [4, 5] – which are typically referred to as “replicator dynamics” in the evolutionary dynamics literature [23]. Curiously, however, Mehta et al. [12] made the discovery that these dynamics lead in the long run (in almost all cases) to a genetic monoculture. This rather contradicts the evidence of natural diversity around us.

Several plausible explanations exist for this discrepancy, including: (a) mutations [13], (b) speciation (*e.g.*, the Bateson-Dobzhansky-Muller model) [9], (c) the mathematical assumptions are too far from reality, (d) “in the long run” is longer than geologic time. There is, however, a long-standing argument, that there is another (and perhaps more important) factor driving diversity; to our knowledge this case was first compellingly laid out by Ehrlich and Raven in 1964 [6]: “It is apparent that reciprocal selective responses have been greatly underrated as a factor in the origination of organic diversity.” (Already Darwin noted the significance of co-evolution, *e.g.*, between orchids and moths that feed on their nectar; but the proposed implication for diversity seems to have come later.) In the ensuing decades this idea played a role in the *Red Queen Hypothesis* [21] and was advanced as an explanation of an advantage of sexual over asexual reproduction [1].

Apart from empirical study (*e.g.*, [3, 20, 16, 2]), the dynamics of co-evolution have also been studied mathematically, but primarily (explicitly or implicitly) for asexual reproduction – dynamics in which the abundance of a genome changes over time in proportion to its fitness (possibly with mutations), as in the work of Eigen, Schuster and others [7, 8, 15, 18, 19]. The case of sexual reproduction, however, is quite different. There is a good mathematical model for these dynamics, called the “weak selection” model [14], but effects of co-evolution are not yet understood in this model.

We study a specific class of systems in this model, and provide a quantitative study of the evolutionary dynamics of sexual species in highly competitive (“zero sum”) interactions. This study supports the thesis of Ehrlich and Raven, that competition drives diversity, in a strong form: not only does a genetic monoculture not take over, but in fact the entropy of the species’ genomes is bounded away from 0 for all time. Thus we support a rationale for ecosystem diversity without invoking mutation, speciation or environmental change.

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