Algorithms, games, and evolution

Erick Chastain, Adi Livnat, Christos Papadimitriou, and Umesh Vazirani

Abstract

Even the most seasoned students of evolution, starting with Darwin himself, have occasionally expressed amazement that the mechanism of natural selection has produced the whole of Life as we see it around us. There is a computational way to articulate this amazement: “What algorithm could possibly achieve all this in a mere three and a half billion years?” In this paper we propose an answer: We demonstrate that in the regime of weak selection, the standard equations of population genetics describing natural selection in the presence of sex become identical to those of a repeated game between genes played according to multiplicative weight updates (MWUA), an algorithm known in computer science to be surprisingly powerful and versatile. MWUA maximizes a tradeoff between cumulative performance and entropy, which suggests a new view on the maintenance of diversity in evolution.
We now introduce the framework of game theory (see Fig. 2 for an illustration) and the MWUA (SI Text), studied in computer science and machine learning, and rediscovered many times over the past half-century; as a result of these multiple rediscoveries, the algorithm is known with various names across subfields: “the experts algorithm” in the theory of algorithms, “Hannan consistency” in economics, “regret minimization” in game theory, “boosting” and “winnow” in artificial intelligence, etc. Here we state it in connection to games, which is only a small part of its applicability (see SI Text for an introduction to the MWUA in connection to the so-called “experts problem” in computer science).

A game has several players, and each player $i$ has a set $A_i$ of possible actions. Each player also has a utility, capturing the way whereby her actions and the actions of the other players affect this player’s well-being. Formally the utility of a player is a function that maps each combination of actions by the players to a real number (intuitively denoting the player’s gain, in some monetary unit, if all players choose these particular actions). In general, rather than choosing a single action, a player may instead choose a mixed or randomized action, that is, a probabilistic distribution over her action set. Here we only need to consider coordination games, in which all players have the same utility function—that is, the interests of the players are perfectly aligned, and their only challenge is to coordinate their choices effectively. Coordination games are among the simplest games; the only challenge in such a game is for the players to “agree” on a mutually beneficial action.

How do the players choose and adjust their choice of randomized (mixed) actions over repeated play? Assume that at time $t$, player $i$ has mixed action $x_i^t$ assigning to each action $j \in A_i$ the probability $x_i^t(j)$. The MWUA algorithm (5) adjusts the mixed strategy for player $i$ in the next round of the game according to the following rule:

$$x_i^{t+1}(j) = \frac{1}{Z_t} u_i^t(j)(1 + \varepsilon u_i^t(j)).$$

where $Z_t$ is a normalizing constant designed to ensure that $\sum x_i^{t+1}(j) = 1$, so $x_i^{t+1}$ is a probability distribution; $\varepsilon$ is a crucial small positive parameter, and $u_i^t(j)$ denotes the expected utility gained by player $i$ choosing action $j$ in the regime of the mixed actions by the other players effective at time $t$. This algorithm $(i)$ is known to converge to the min–max actions if the game is two-player zero-sum; $(ii)$ is also shown here to converge to equilibrium for the coordination games of interest in the present paper (SI Text, Corollary 3); $(iii)$ is a general “learning algorithm” that has been shown to be very successful in both theory and practice; and $(iv)$ if, instead of games, it is applied to a large variety of optimization problems, including linear programming, convex programming, and network congestion, it provably converges to the optimum quite fast.

It can be now checked that the two processes expressed in Eqs. 1 and 2, evolution under natural selection in the presence of sex and multiplicative weight updates in a coordination game, are mathematically identical (SI Text, Theorem 3). That is, the interaction of weak selection and sex is equivalent to the MWUA in a coordination game between loci in which the common utility is the differential fitness of the organism. The parameter $\varepsilon$ in the algorithm, which, when small signifies that the algorithm is taking a “longer-term view” of the process to be solved (SI Text), corresponds to the selection strength in evolution, i.e., the magnitude of the differences between the fitness of various genotypes.

The MWUA is known in computer science as an extremely simple and yet unexpectedly successful algorithm, which has surprised us time and again by its prowess in solving sophisticated computational problems such as congestion minimization in networks and convex programming in optimization. The observation that multiplicative weight updates in a coordination game are equivalent to evolution under sex and weak selection makes an informative triple connection between three theoretical fields:

$$x_i^{t+1}(j) = \frac{1}{Z_t} u_i^t(j)(1 + \varepsilon u_i^t(j)).$$

Fig. 1. Equations of population genetics formulated in the 1930s constitute the standard mathematical way of understanding evolution of a species by tracking the frequencies of various genotypes in a large population. In the simple example shown here, a haploid organism with two genetic loci $A$ and $B$ has three alleles in each of its two loci named $A_1$, $A_2$, $A_3$ and $B_1$, $B_2$, $B_3$ for a total of nine genotypes. In $A$ we show the fitness of each genotype, that is, its expected number of offspring. The fitness numbers shown in $A$ are all close to each other, reflecting weak selection, where the individual alleles’ contributions to fitness are typically minuscule. Initially, each genotype occurs in the population with some frequency; in this particular example these numbers are initially equal (8); naturally, their sum over all nine genotypes is 1 (frequencies are truncated to the fourth decimal digit). $C$ shows how the genotype frequencies evolve in the next generation: each individual of a given genotype produces a number of offspring that is proportional to its fitness shown in $A$, and the resulting offspring inherits the alleles of its parents with equal probability (because we are assuming, crucially, sexual reproduction). The genotype frequencies in the next generation are shown in $C$, calculated through the standard recurrence equations of population genetics. We also show in the margins of the table the allele frequencies, obtained by adding the genotype frequencies along the corresponding row or column. Ten generations later, the frequencies are as shown in $D$. 

A | B1 | B2 | B3
---|---|---|---
A1 | 1.02 | 1.03 | 0.99
A2 | 1.00 | 1.01 | 0.98
A3 | 1.01 | 1.04 | 1.02

Fitness values

<table>
<thead>
<tr>
<th>C</th>
<th>0.3330</th>
<th>0.3385</th>
<th>0.3286</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.3341</td>
<td>0.1112</td>
<td>0.1131</td>
<td>0.1098</td>
</tr>
<tr>
<td>0.3286</td>
<td>0.1094</td>
<td>0.1112</td>
<td>0.1080</td>
</tr>
<tr>
<td>0.3374</td>
<td>0.1123</td>
<td>0.1142</td>
<td>0.1108</td>
</tr>
</tbody>
</table>

Genotype and allele frequencies after 1 generation

B | 0.3333 | 0.3333 | 0.3333
---|---|---|---
| 0.3333 | 0.1111 | 0.1111 | 0.1111 |
| 0.3333 | 0.1111 | 0.1111 | 0.1111 |
| 0.3333 | 0.1111 | 0.1111 | 0.1111 |

Initial genotype and allele frequencies

D | 0.3266 | 0.3860 | 0.2874
---|---|---|---
| 0.3396 | 0.1109 | 0.1311 | 0.0976 |
| 0.2871 | 0.0938 | 0.1108 | 0.0825 |
| 0.3733 | 0.1219 | 0.1441 | 0.1073 |

Genotype and allele frequencies after 10 generations
The first term is the current (at time \( t \)) expected cumulative utility. The second term of \( 3 \) is the entropy (expected negative logarithm) of the probability distribution \( \{x_i(j), j = 1, \ldots, |A_i|\} \), multiplied by a large constant \( 1/\epsilon \). Suppose now that player \( i \) wished to choose the probabilities of actions \( x_i(j) \)'s with the sole goal of maximizing the quantity \( 3 \). This is a relatively easy optimization problem, because the quantity \( 3 \) to be maximized is strictly concave, and therefore it has a unique maximum, obtained through the Karush–Kuhn–Tucker conditions of optimality (8) (SI Text, section 4):

\[
U_i(t) = \sum_j x_i(j)U_i(j) - \frac{1}{\epsilon} \sum_j x_i(j) \ln x_i(j). 
\]

The first term is the current (at time \( t \)) expected cumulative utility. The second term of \( 3 \) is the entropy (expected negative logarithm) of the probability distribution \( \{x_i(j), j = 1, \ldots, |A_i|\} \), multiplied by a large constant \( 1/\epsilon \). Suppose now that player \( i \) wished to choose the probabilities of actions \( x_i(j) \)'s with the sole goal of maximizing the quantity \( 3 \). This is a relatively easy optimization problem, because the quantity \( 3 \) to be maximized is strictly concave, and therefore it has a unique maximum, obtained through the Karush–Kuhn–Tucker conditions of optimality (8) (SI Text, section 4):

\[
U_i(t) = \sum_j x_i(j)U_i(j) - \frac{1}{\epsilon} \sum_j x_i(j) \ln x_i(j). 
\]

The first term is the current (at time \( t \)) expected cumulative utility. The second term of \( 3 \) is the entropy (expected negative logarithm) of the probability distribution \( \{x_i(j), j = 1, \ldots, |A_i|\} \), multiplied by a large constant \( 1/\epsilon \). Suppose now that player \( i \) wished to choose the probabilities of actions \( x_i(j) \)'s with the sole goal of maximizing the quantity \( 3 \). This is a relatively easy optimization problem, because the quantity \( 3 \) to be maximized is strictly concave, and therefore it has a unique maximum, obtained through the Karush–Kuhn–Tucker conditions of optimality (8) (SI Text, section 4):

\[
U_i(t) = \sum_j x_i(j)U_i(j) - \frac{1}{\epsilon} \sum_j x_i(j) \ln x_i(j). 
\]
This new way of understanding the maintenance of variation in evolution (selection as a tradeoff between fitness and entropy maximization) is quite different from previous hypotheses for the maintenance of variation (e.g., refs. 11, 12). Another rather surprising consequence of this characterization is that, under weak selection, all past generations, no matter how distant, have equal influence on the change in the allele mix of the current generation.

Our discussion has focused on the evolution of a fixed set of alleles; that is, we have not discussed mutations. Mutations are, of course, paramount in evolution, as they are the source of genetic diversity, and we believe that introducing mutations to the present analysis is an important research direction. Here we focus on the selection process, which is rigorously shown to be tantamount to a tradeoff, for each locus, between maximizing diversity and maximizing expected cumulative fitness.

We can now note a simple yet important point. Because multiplicative weight updates by the loci operate in the presence of sex, the triple connection uncovered in this paper is informative for the “queen of problems in evolutionary biology,” namely the role of sex in evolution (13, 14). The notion that the role of sex is the maintenance of diversity has been critiqued (15), because sex does not always increase diversity, and diversity is not always favorable. The MWUA connection sheds new light on the debate, because sex is shown to lead to a tradeoff between increasing entropy and increasing (cumulative) fitness.

The connection between the three fields, evolution, game theory, and learning algorithms, described here was not accessible to the founders of the modern synthesis, and we hope that it expands the mathematical tracks that can be traveled in evolution theory.

ACKNOWLEDGMENTS. We thank Satish Rao, Noam Nisan, and Monty Slatkin for helpful discussions and comments, and the visitors of the Spring 2014 program on Evolutionary Biology and Computation at the Simons Institute for the Theory of Computing for engaging discussions. Special thanks are due to Nick Barton for his constructive criticism of an earlier version, which led to several important improvements of our presentation, including the correction of a potentially confusing oversight. The research of E.C. was supported by National Science Foundation Grant CCF-1064785. The research of C.P. was supported by National Science Foundation Grant CCF-0964033, and by Templeton Foundation Grant 39966. The research of U.V. was supported by National Science Foundation Grant CCR-0905626.