

Differences in the concept of fitness between artificial evolution and natural selection

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Extended Abstract

Evolutionary algorithms were proposed to automatically find solutions to computational problems, much like evolution discovers new adaptive traits (Fogel et al., 1966). Lately, they have been used to address challenging questions about the evolution of modularity (Kashtan et al., 2007), the genetic code (Vetsigian et al., 2006), communication (Floreano et al., 2007), division of labor (Lichocki et al., 2012) and cooperation (Riolo et al., 2001; Waibel et al., 2011). Evolutionary algorithms are increasingly popular in biological studies, because they give precise control over the experimental conditions (Floreano and Keller, 2010) and allow the study of evolution at unprecedented level of detail (Adami, 2006). Nevertheless, evolutionary algorithms have their own caveats, which are often overlooked. Here, we highlight one of them by exposing a terminological conflict between definitions of fitness used in biology and in evolutionary algorithms.

Fitness is a core concept in evolutionary biology (Wagner, 2010). Although used to mean subtly different things (Orr, 2009), it is commonly agreed that fitness is a variable that describes competitive abilities of a given genotype against others in a population under some environmental conditions (Wagner, 2010). The understanding of fitness is very well captured in selection equations (Fisher, 1930; Wright, 1969), where the relative fitness, i.e., the ratio between a fitness value and the mean fitness in a population, directly translates into a proportionate reproductive success. Consequently, only relative fitness bears meaning, i.e., all fitness values may be scaled by the same constant and the evolutionary dynamics would remain the same (Wagner, 2010). For convenience, fitness is usually taken to be the expected or realized number of offspring (Rice, 2004; Orr, 2009).

In contrast to biology, in evolutionary algorithms the term fitness does not usually refer to the reproductive success. Instead, fitness means the performance of a given genotype in solving a given problem. For example, if a genotype encodes a control system that guides a robot's movement in a labyrinth, its performance could be measured as the time needed to find the exit. Once all genotypes are evaluated, they are selected according to their performance val-

ues, and then copied and varied. Several popular selection methods exist: proportionate selection (Goldberg (1989); or roulette wheel selection; used by Waibel et al. (2011)), truncation-proportionate selection (used by Lichocki et al. (2012)), truncation selection (Schlierkamp-Voosen (1993); or (μ, λ) -selection (Back, 1994); used by Floreano et al. (2007); Kashtan et al. (2007)), rank selection (Baker, 1985) and tournament selection (Goldberg and Deb (1991); used by Riolo et al. (2001)).

Here, we experimentally and formally show that the reproductive success of genotypes is proportional to the performance only with proportionate selection. Consequently, only then a genotype's performance, called fitness by evolutionary algorithms practitioners, is actually fitness in the biological sense. All other selection methods introduce a non-linear transformation of performance values into reproductive success. Thus, in all these cases performance is not fitness in the biological sense. This observation has a limited practical meaning in engineering application, where the goal is to find optimal solution to a problem. Usually, the best suited selection method is used and terminological issues are not of any relevance.

In contrast, in biological studies that rely on evolutionary simulations a clear distinction between performance and fitness is necessary for a meaningful interpretation. We support this claim with numerical experiments in which we conducted 1000 generations of artificial selection in groups of agents. Each agent displayed selfish or altruistic behavior towards its teammate. We show that the outcome of the evolutionary simulations of cooperation (i.e., emergence of reproductive division of labor) depends on the selection method and its parameters (Fig. 1).

We considered the evolution of cooperation as our model system, because evolutionary algorithms are a popular tool in this domain (see, e.g., Riolo et al. (2001); Floreano et al. (2007); Waibel et al. (2011)). In the evolution of cooperation, the crucial concepts are cost and benefit of a cooperative act. Importantly, these cost and benefit of cooperation are additive to fitness. In contrast, an experimenter who uses evolutionary simulations may influence costs and benefits

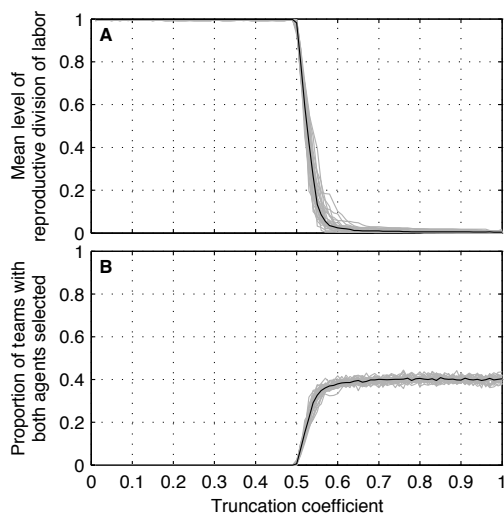


Figure 1: (A) Mean level of reproductive division of labor in population of 500 teams, each consisting of two agents. (B) Proportion of teams in the generation 999 that contributed both agents to the last 1000th generation. Each agent was assigned one performance point by default, and then could transfer it to its partner in the team. The team displayed reproductive division of labor when one agent was selfish, i.e., kept the performance point to itself, and the other agent was altruistic, i.e., gave its performance point to the partner. The evolutionary simulation was replicated 30 times for each of the 100 treatments (truncation coefficient was set to a value from 0.01 to 1, with a step of 0.01). The result of each replicate is shown in grey.

additive to performance. Consequently, in order to validate the predictions of biological models of cooperation, a correction for the selection method must be applied to fitness, in the case of a non-proportionate selection. Alternatively, one may use proportionate selection. Then, performance is fitness, and cost and benefit additive to performance are automatically additive to fitness. Note, however, that proportionate selection is known to display several disadvantageous properties, e.g., premature convergence (Baker, 1987).

Overall, we call for caution when using evolutionary algorithms in biological studies and advise to carefully account for effects that a selection method has on the fitness landscape.

Acknowledgments

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