Opportunistic gambling versus conservative bet-hedging in populations evolving in fluctuating environments

Rubén Calvo[1,2], Miguel A Muñoz[1,2], and Tobias Galla[3]
[1]Departamento de Electromagnetismo y Física de la Materia, Universidad de Granada E-18071, Granada, Spain
[2] Instituto Carlos I de Física Terica y Computacional, Universidad de Granada E-18071, Granada, Spain
[3] Instituto de Física Interdisciplinar y Sistemas Complejos IFISC (CSIC-UIB), 07122 Palma de Mallorca, Spain

Living organisms often have to struggle with the variability of their surroundings. When environmental fluctuations are unpredictable, lineages of individuals can prevail if genotypes 'hedge their bets' [1]. The theory of bet hedging states that evolutionary success is determined not only by the mean fitness of a certain population but rather by a trade-off between such an average fitness (first moment of the distribution, denoted as μ) and the fitness variation across environmental conditions (second moment of the distribution, denoted as σ^2). However, higher order moments of the distribution of fitness have not yet been taken into account, and the impact of asymmetry on the success of bet-hedging strategies remains unknown.

Here, we aim to study precisely the effect that the shape of the distribution of fitness has on the benefits of adopting a bet-hedging strategy. For that, we propose a Stochastic Evolutionary Game Theory approach [2] and use an individual-based model for a finite population, considering the situation in which a single mutant needs to thrive in an established existing resident population. The dynamics unfolds through a series of stochastic birth-death events, where the reproduction rates of residents and mutants are controlled by their payoffs, that fluctuate stochastically according to a certain distribution (see Figure 1). With these ingredients, the population dynamics are such that the mutant will eventually either go extinct or take over the population. Hence, the success of a newly introduced mutant can be quantified in terms of the probability of fixation, denoted as ϕ_1.

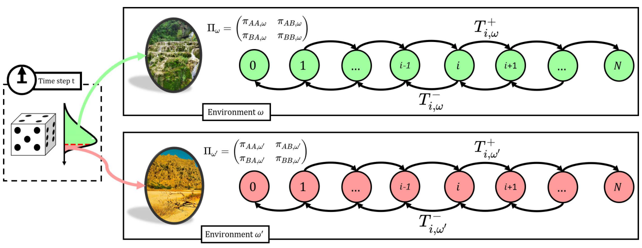

Fig. 1. **Illustration of the model.** A Stochastic Evolutionary Game in which the payoffs are drawn, at each birth-death event, out of a certain distribution. The environment is denoted as ω. The payoff matrix is an environment-dependent function denoted as Π_ω. The state of the system is characterized by the number of individuals adopting the strategy A, i. The transition probabilities $T^{\pm}_{i,\omega}$ denote the probabilities of each birth-death event. N denotes the total size of the population.

Using this simple model, we were able to prove, both numerically and analytically that the Evolutionary Stable Strategy (that is, the strategy that cannot be invaded with a probability bigger than $1/N$) is determined not only by the mean fitness and its variance but also by the shape of the distribution and, more specifically, by its degree of asymmetry, quantified by the skewness μ_3. The simplest case comes when we suppose that the payoff of the individual adopting strategy A is a_1 with probability p_1 and a_2 with probability p_2, while the individual adopting strategy B always receives a payoff equal to 1 (because the outcome of the game only depends on payoff differences, one of the payoffs can always be set to 1). For this scenario, the fixation probability in terms of the first three moments is depicted in Figure 2. In this case, we can observe the existence of bet-hedging strategies in which the values of σ and μ are reduced and the fixation probability ϕ_1 increases; together with what we have named 'opportunistic gambling strategies', being those in which the evolutionary success is increased by increasing the variance of the fitness distribution, rather than reducing it.

This work stands as an initial point to study the relevance of the asymmetry on the distribution of payoffs to determine the evolutionary success of bet-hedging strategies. A more sophisticated model would include the separation of time scales for the evolutionary process and the stochastic switching of the environment.

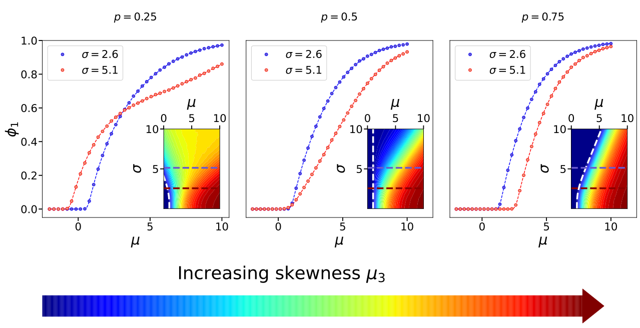

Fig. 2. **Results for a dichotomous distribution of payoffs**: The graphs show the fixation probability in terms of the first moment μ for two different values of σ (circles are the results of the simulations, the lines come from the theory), each for a certain value of the probability p_1 (and hence, a certain skewness). The insets show the fixation probability in the space (μ, σ). The white dotted line in the inset stands for the frontier of the Evolutionary Stable Strategy.

[1] Starrfelt, Jostein and Kokko, Hanna, *Bet-hedging-a triple trade-off between means, variances and correlations*, Biological Reviews 87, 14647931 (2012).

[2] P. Ashcroft, P. M. Altrock, and T. Galla, *Fixation in finite populations evolving in fluctuating environments*, J. R. Soc. Interface., vol. 11, no. 100, p. 20140663, Nov. 2014, doi: 10.1098/rsif.2014.0663.