

Editorial

## ESS theory now

More than 30 years have passed since the concept of evolutionarily stable strategy (ESS) was introduced in the context of animal conflicts (Maynard Smith and Price, 1973). Where the theory stands nowadays is the theme of this issue.

At the very beginning, necessary and sufficient conditions for a strategy to be evolutionarily stable were given in the exemplified framework of matrix games that stem from pairwise interactions between individuals adopting mixed strategies defined over a given finite set of pure strategies. An important feature of matrix games is the underlying linear fitness functions that they engender. Although these can be best viewed as linear approximations of more general functions, matrix games manage to capture the essence of the ESS concept. Even today the main idea, and the more general one, remains to look for a population equilibrium, often a fixation state, that can resist the invasion of any rare mutant. Such population states are the only ones that can be maintained, and therefore observed, in the long run as new mutants are introduced into the population. The approach can be applied to any selection model with any population structure, which explains its durable success. From a practical point of view, however, the question of interest is often to identify the factors that can explain the evolution and the maintenance of behavioral traits, for example, cooperation, or genetic mechanisms (e.g., recombination) that may incur individual costs.

Very early, the need to grasp the global dynamics, and therefore to ascertain the long-term evolution towards an ESS, led to the extended concept known as continuously stable strategy (CSS), which adds the condition that a population equilibrium, or at least a fixation state, close enough to the ESS is invaded only by mutants that bring the population even closer (Eshel and Motro, 1981). This condition alone is sometimes more useful than the ESS condition itself since ESS analyses often degenerate and show only neutrality of any mutant. Several related conditions and dynamical properties have been proposed later on, some under genetic constraints, e.g., for matrix games and the sex ratio game. Although one expects the evolution of the population state towards a phenotypic equilibrium corresponding to an ESS as new mutants are introduced, such a global evolutionary scheme in exact

population genetic models has been proved rigorously or suggested by local stability analyses only in a few cases and shown by simulations not to be necessarily monotone even over successive equilibria reached by the population. Considering random drift, which cannot be neglected when the population size is small, any mutant can go to fixation, and long-term evolution or adaptive dynamics has to be defined in probabilistic terms, and this opens new perspectives. (See Lessard, 2005, and references therein.)

The contributors to this issue address questions of current interest in ESS theory, some related to matrix games or the evolution of cooperation, others to non-linear frequency-dependent selection or adaptive dynamics.

Joseph Apaloo revisits, in the context of matrix games, the concept of neighborhood invader strategy (NIS), which is the property for a mutant strategy to invade any other population strategy. It is shown that such a strategy cannot coexist with an ESS unless it is itself an ESS (called an ESNIS), and then it is globally asymptotically stable with respect to the mixed strategies of full support under the replicator dynamics at least if it is itself of full support or corresponds to a pure strategy.

Christine Taylor and Martin Nowak consider interaction rates that depend on the strategies used by the individuals. This introduces non-linear fitness functions in the replicator equation. The game dynamics is described completely in the case of two strategies and the results applied to the Prisoner's Dilemma and the Snow-Drift game. It is shown that, if one of the strategies dominates the other, then non-uniform interaction rates can introduce a pair of interior equilibria.

Ross Cressman extends the uninvasibility concept to  $N$ -species models of frequency-dependent evolution. The main result is that the resident state is uninvasible if some mutant strategy of a small monomorphic mutant subpopulation is less fit than the resident strategy in at least one species. This is established for discrete or continuous time models and connected to the  $N$ -species matrix-ESS concept when the fitness functions are linear.

Ulf Dieckmann and Hans Metz show that more realistic ecological scenarios in selection models may result in qualitatively different outcomes. This is illustrated by: (1) the loss of evolutionary neutrality when matrix games are unfolded by introducing density regulation and variable

rewards or variable interaction rates; (2) the extinction of populations under frequency- and density-dependent selection when the trait, e.g., body size, has opposite effects on competition and fecundity; (3) the failure of optimization principles based on the reproductive ratio of a disease in predicting evolutionary outcomes in epidemiological models unless restrictive conditions on the environmental feedback are satisfied; and (4) the non-occurrence of Hardy–Weinberg proportions in sex-structured populations in generic cases under genetic constraints.

Carlo Matessi and Alexander Gimelfarb investigate frequency-dependent disruptive selection on a continuous trait determined, precisely or randomly, at a single multi-allelic locus. They manage to show, numerically and analytically, long-term evolution towards a phenotypic equilibrium exhibiting maximal variance, which occurs when only two extreme phenotypes are present. Moreover, as long as this equilibrium is not reached, there is a long-term increase in the variability of genetic expression.

François Rousset deduces the probability of fixation of a mutant under isolation by distance from the expected change in the allele frequency from one generation to the next. Regular lattice models are considered and approximations are made under the assumptions of a large number of finite demes and intermediate allele frequencies under weak selection. These allow to compute second moments under neutrality and to use a separation of time scale to make appeal to a quasi-equilibrium argument. The results are illustrated by simulations for mutants affecting the probability of dispersal in a circular stepping-stone model.

Nicolas Champagnat, Régis Ferrière and Sylvie Méléard start with a stochastic individual-based model in which the adaptive traits of individuals affect their birth and death rates, the mutation process, and how they interact with each other and their environment. By applying various renormalizations and advanced probabilistic tools, they prove convergence to different macroscopic models. The large-population limit extends Kimura's continuum-of-alleles model to the case of frequency- and density-dependent selection. A separation of time scale is obtained by accelerating births and deaths while diminishing mutational effects and leads to a generalization of Fisher's reaction–diffusion equation. When mutation becomes very rare, the population remains monomorphic and the trait evolves according to a jump process, which underlies the adaptive dynamics approach.

Peter Taylor and co-workers study the effect of plasticity in host–pathogen systems when one of the interacting partners acts first and then the other can respond to this information (precedence) or when both partners can respond to the strategy adopted by the other (negotiation). In both cases the pathogen-induced mortality rate (virulence) and the rate at which the infected host recovers from infection (clearance) exhibited at the Nash equilibrium show a decrease. It is concluded that phenotypic plasticity provides a mechanism whereby positive correlations

between interacting partners leading to higher levels of cooperation may arise. This raises another question: why cooperative outcomes should evolve?

Ross Hammond and Robert Axelrod use agent-based simulation to show that contingent altruism based on tags (cooperate with those who share the same tag) can evolve in a viscous environment with individuals interacting only with their adjacent neighbours even when altruism is expensive (high cost/benefit ratio) and tags are not linked to altruism. This illustrates how agent-based simulation allows for the analysis of biological settings which cannot be characterized by simple pairwise approximations typical of ESS analysis and suggests new mechanisms for the evolution of cooperation to explore.

Edward Hagen and Peter Hammerstein critically review some recent interpretations of experimental economic games such as the ultimatum game suggesting that humans may not conform to Nash equilibrium predictions in the context of strategic interaction. In order to explain strong reciprocity, for instance, which is defined as cooperation with cooperative individuals and punishment of non-cooperative individuals, even at personal cost, one commonly resorts to cultural group selection of 'other regarding' social norms acquired either by conformist transmission or prestige-biased transmission. This assumes that humans are rational actors seeking to maximize some population utility function. It is rather proposed that the explanation may rely on the cognitive frames used by the individuals to interpret their experiences.

I am most grateful to all the authors for these remarkable contributions. I want also to thank all the reviewers whose expertise and help have contributed to the quality of this issue. Finally, I thank Samuel Karlin for giving me the opportunity to take on this special project on ESS theory. I owe to Ilan Eshel, Marcus Feldman, and especially Samuel Karlin, who has been an extraordinary mentor, my first acquaintance with evolutionary stability in the context of sex ratio evolution in Mendelian populations (Karlin and Lessard, 1986). The concept is now used in a very wide variety of contexts and has matured. It has inspired not only population biologists but also applied mathematicians and social scientists. It was an appropriate time to take a pause and ask ourselves what ESS theory means today. Following the John Maynard Smith memorial issue in which the influence of one of its founders was recalled, the present sample of subjects and authors does not pretend to be exhaustive but I do believe that it is representative of the recent advances and active searchers in the field.

## References

- Eshel, I., Motro, U., 1981. Kin selection and strong evolutionary stability of mutual help. *Theor. Popul. Biol.* 19, 420–433.
- Karlin, S., Lessard, S., 1986. *Theoretical Studies on Sex Ratio Evolution*. Princeton University Press, Princeton.

- Lessard, S., 2005. Long-term stability from fixation probabilities in finite populations: new perspectives for ESS theory. *Theor. Popul. Biol.* 68, 19–27.
- Maynard Smith, J., Price, J.R., 1973. The logic of animal conflict. *Nature* 246, 15–18.

Sabin Lessard\*  
*Département de mathématiques et de statistique, Université  
de Montréal, Montréal, Québec, Canada H3C 3J7  
E-mail address: lessards@dms.umontreal.ca.*

---

\*Tel.: +1 514 343 6743; fax: +1 514 343 5700.