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Polymorphic Evolutionary Games

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HIGHLIGHTS

- Natural selection acts on the phenotypic differences, evolution depends on the genetic transmission of these differences from one generation to the next.
- Since phenotypic selection is subject to genetic constraints, some population geneticists perceive *evolutionary game theory* (EGT) with skepticism.
- I present an analytical extension of the evolutionary game theory that allows explicit modeling of the underlying genetics—*polymorphic EGT* (PEGT).
- In particular, PEGT can be used to model long-term evolution in explicitly genetic terms.

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ABSTRACT

In this paper, I present an analytical framework for polymorphic evolutionary games suitable for explicitly modeling evolutionary processes in diploid populations with sexual reproduction.

The principal aspect of the proposed approach is adding diploid genetics cum sexual recombination to a traditional evolutionary game, and switching from *phenotypes* to *haplotypes* as the new game's pure strategies. Here, the relevant pure strategy's payoffs derived by summing the payoffs of all the phenotypes capable of producing gametes containing that particular haplotype weighted by the pertinent probabilities.

The resulting game is structurally identical to the familiar *Evolutionary Games with non-linear pure strategy payoffs* (Hofbauer and Sigmund, 1998. Cambridge University Press), and can be analyzed in terms of an established analytical framework for such games. And these results can be translated into the terms of genotypic, and whence, phenotypic evolutionary stability pertinent to the original game.

A zygote is a gamete's way of producing more gametes.

Robert Anson Heinlein

1. Introduction

Game Theory is a branch of mathematics analyzing conflicts of interest where the participants, *players*, have a choice of several distinct ways to act—*pure strategies*. The players are not restricted to using pure strategies, and can play combinations of pure strategies with specific frequency assigned to each—*mixed strategies*. Thus, every player has a spectrum of possible responses, and the optimal choice for each depends on the choices made by all the others. Classical game theory deals with human economic behavior i.e., the utility scale is that of financial gain, and the players are assumed to be rationally selfish.

In the adaptation of game theory to evolutionary research—*evolutionary game theory* (EGT), emphasis was shifted from individuals to populations, financial gain was replaced by *Darwinian fitness*, and the term strategy came to refer to a heritable phenotype. Finally, rational decision-making was replaced by *evolutionary stability*—a heritable phenotype is an *evolutionarily stable strategy* (ESS) if the players of this strategy have higher fitness than players of any pertinent alternative strategy when the preponderance of the ESS players is sufficiently large (Smith and Price, 1973).

However, investigation of evolutionary processes by EGT methods proceeds under a serious handicap. To wit, while pure strategies purported to represent heritable phenotypes—the heritability in question is *monomorphic*. That is, all of an individual's offspring are copies of itself—an attribute that is not optimal for modeling evolution in diploid populations with sexual recombination.

The fact that, despite the above handicap, EGT played a profound role in the development of modern Ecological and Evolutionary Theories (cf. Begon et al., 1990; Alcock, 1993; Krebs and

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Davies, 1993), is a testament to the strengths of the EGT approach. Nevertheless, the desirability of having *polymorphic* evolutionary games as a research tool is undisputable. Below I provide an analytical framework for such games.

In the proposed approach, we start by associating a conventional (phenotypic) evolutionary game with a plausible diploid genetic model.[1] The next step is defining the appropriate pure strategies.

- While the idea of adopting distinct genotypes as pure strategies is intuitively appealing, upon closer examination it is untenable. For example, barring special cases, the frequency of every heterozygous genotype is the geometric mean of the frequencies of the two appropriate homozygous genotypes.
- The last observation, however, suggests the use of haplotypes as the polymorphic game's pure strategies—an approach that, in hindsight, seems to be self-evident. After all, while a diploid individual is the unit of selection—it only passes half of its genes to each descendant. Note: a mixed strategy in this haplotypic context corresponds to population level polymorphism in the original game.

In this, *haplotypic*, approach the relevant pure strategy payoffs are derived by summing the fitness of all the phenotypes capable of producing gametes containing the haplotype in question weighted by the pertinent probabilities. Details such as allelic segregation probabilities, gametic competition etc., can be incorporated into the formulations at this stage, as necessary.

The resulting game is structurally analogous to *symmetric* evolutionary games with *non-linear* pure strategy payoffs—*SNL games* (Hofbauer and Sigmund, 1998; Fishman, 2003, 2008). Accordingly, this paper is organized as follows:

In Section 2, I detail the process of transforming a monomorphic – into a polymorphic evolutionary game. Section 3 presents an example of the methodology: a polymorphic game based on the well-known Tit-for-Tat/ Defector/Unconditional Altruist model of Selten and Hammerstein (1984). I chose this particular example because, in addition to being well known, it illustrates the fact that adding explicit genetics to an evolutionary game may suggest novel research directions.

To assure both the compactness and the completeness of the paper, some of the necessary technical details confined to the appendixes, collected into an electronic supplement.

- Appendix A comprises a brief survey of the attributes of SNL games that distinguish them from the, more familiar, *symmetric linear* (SL) evolutionary games.
- Appendix B details the evolutionary stability analysis for the game in Section 3.
- Finally, in Appendix C, I show that for two-phenotype games polymorphic and monomorphic approaches yield identical results.

2. Basic theory

Let us postulate a symmetric evolutionary game with m pure strategies: $\sigma_1,\ldots,\sigma_m$; an $m\times m$ payoff matrix $\mathrm{M}\equiv(\mu_{ij})$; and a *strategy set* $\mathbf{X}=\{(x_1,\ldots,x_m)^t\in[0,1]^m|\ \sum x_i=1\}$.

Next, let us assume that this monomorphic game can be plausibly associated with a diploid genetic model exhibiting l genetic loci where the i^{th} locus contains r_i distinct alleles: $A_{i1},\ldots,A_{ir_i}$. Thus, we have $n=r_1\cdot\ldots\cdot r_l$ distinct pertinent *haplotypes* (gamete types); and $N=\frac{n}{2^l}\prod_{i=1}^{l}(r_i+1)$ distinct pertinent *genotypes*. In this formulation, each pure strategy of the original game is equivalent to a *phenotype* associated with a unique set of genotypes.

Let us arrange the n possible haplotypes in a convenient order, and denote them by $\gamma_1,\ldots,\gamma_n$. Let us define the frequency of the γ_j by y_j, and let this polymorphic game's strategy set be $\mathbf{Y}=\{\mathbf{y}=(y_1,\ldots,y_n)^t\in[0,1]^n|\ y_1+\ldots+y_n=1\}$.

Since every phenotype is composed of genotypes, and every genotype is composed of two haplotypes, phenotypic frequencies: $x_1,\ldots,x_m$; can be expressed as a function of haplotype frequencies. That is, exists ψ: $\mathbf{Y}\rightarrow\mathbf{X}$ such that

$$\forall\mathbf{x}\in\mathbf{X},\ \exists\ \mathbf{y}\in\mathbf{Y}\ni\ \mathbf{x}=\psi(\mathbf{y}). \tag{1.1a}$$

Where $\psi(\cdot)$ is onto, but (not necessarily) one–one. In particular, since every genotype can be constructed by combining two haplotypes, we can define (not unique) functional matrix $R(\mathbf{y})$ such that

$$\forall\mathbf{y}\in\mathbf{Y}\ :\ \psi(\mathbf{y})=\mathrm{R}(\mathbf{y})\circ\mathbf{y}. \tag{1.1b}$$

Let $\{\mathbf{d}_1,\ldots,\mathbf{d}_m\}$ and $\{\mathbf{e}_1,\ldots,\mathbf{e}_n\}$ be the respective standard bases of $\mathbf{R}^m$ and $\mathbf{R}^n$. In these terms, the (*per capita*) payoff for playing the j^{th} strategy of the original game, calculated in terms of haplotype frequencies, is given by

$$\mu_j(\mathbf{y})=\mathbf{d}_j\circ\mathrm{M}\circ\mathrm{R}(\mathbf{y})\circ\mathbf{y}. \tag{1.1c}$$

Let $h_{ij}(\mathbf{y})$ denote the probability that a gamete with i^{th} haplotype is produced by an individual of j^{th} phenotype i.e., $h_{ij}(\mathbf{y})=P(\gamma_i\cap\sigma_j)/P(\gamma_i)=P(\sigma_j|\gamma_i)$. As discussed in the introduction, the relevant details of the postulated genetic mechanism e.g. multi-locus recombination etc., are incorporated into the formulations at this stage. Hence, the *per-capita* payoff for playing the i^{th} strategy of the polymorphic game, $\pi_i(\mathbf{y})$, is given by

$$\pi_i(\mathbf{y})=\sum_{j=1}^{m}h_{ij}(\mathbf{y})\mu_j(\mathbf{y}). \tag{1.1d}$$

Consequently, the payoff matrix for the polymorphic game is given by

$$\begin{array}{l}\mathrm{P}(\mathbf{y})=\mathrm{H}(\mathbf{y})\circ\mathrm{M}\circ R(\mathbf{y})\\ \qquad\text{where}\\ \mathrm{H}(\mathbf{y})=\left(h_{ij}(\mathbf{y})\right)_{n\times m}\end{array}. \tag{1.1e}$$

where $\mathrm{H}(\mathbf{y})$ may be thought of as haplotype transmission (probability) matrix.

Remark. A. monomorphic SNL game (cf. Fishman, 2003) can be transformed into a polymorphic SNL game in the same way as an SL game.

3. TfT/defector/unconditional Altruist polymorphic game

Let **UD** stand for *unconditional defector* and **UA** for *unconditional altruist*. The form of the phenotypic game most convenient for current purpose is due to (Lotem et al., 2003).

$$\begin{array}{cc} & \begin{array}{ccc}\textbf{TfT} & \textbf{UD} & \textbf{UA}\end{array}\\ \begin{array}{c}\textbf{TfT}\\ \textbf{UD}\\ \textbf{UA}\end{array} & \begin{pmatrix}B-C & -sC & B-C\\ sB & 0 & B\\ B-C & -C & B-C\end{pmatrix}\end{array}. \tag{2.1}$$

Here $B>0$ are the generic **TfT** player's lifetime benefits of receiving help from another **TfT**, while $C>0$ is the corresponding costs of donating help. Finally, let s denote the probability that a **UD** successfully deceives a **TfT**. A **UD** can successfully deceive a **TfT** at least once—thus, $s>0$. If a **UD** can successfully deceive a **TfT**

[1] In cases when there is more than one possible genetic model, each produces a distinct polymorphic game.