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Games among relatives revisited

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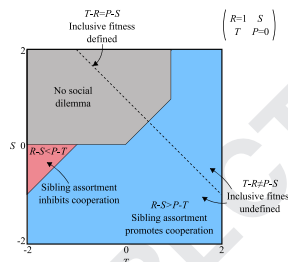
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HIGHLIGHTS

- We introduce a simple model for the evolution of social behavior in a family-structured population.
- We calculate fixation probabilities and success conditions in terms of game payoffs, sibling assortment, and population size.
- Sibling assortment aids cooperation in the Prisoner's Dilemma, but can hinder cooperation in relaxed social dilemmas.
- Inclusive fitness methods do not apply to the general case of our model.
- Inclusive fitness applies in the special case of “equal gains from switching”, but provides less information than an analysis based on gene frequency.

GRAPHICAL ABSTRACT



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ABSTRACT

We present a simple model for the evolution of social behavior in family-structured, finite sized populations. Interactions are represented as evolutionary games describing frequency-dependent selection. Individuals interact more frequently with siblings than with members of the general population, as quantified by an assortment parameter r , which can be interpreted as “relatedness”. Other models, mostly of spatially structured populations, have shown that assortment can promote the evolution of cooperation by facilitating interaction between cooperators, but this effect depends on the details of the evolutionary process. For our model, we find that sibling assortment promotes cooperation in stringent social dilemmas such as the Prisoner's Dilemma, but not necessarily in other situations. These results are obtained through straightforward calculations of changes in gene frequency. We also analyze our model using inclusive fitness. We find that the quantity of inclusive fitness does not exist for general games. For special games, where inclusive fitness exists, it provides less information than the straightforward analysis.

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1. Introduction

In many biological populations, family members interact frequently with each other. Family structure is an important form of

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population structure, which can affect evolution in a variety of ways (Nowak et al., 2010a). For example, spatial or group structure in a population can promote the evolution of cooperative behaviors by allowing cooperators to cluster together and limit exploitation by noncooperators (Nowak and May, 1992; Durrett and Levin, 1994; van Baalen and Rand, 1998; Ohtsuki et al., 2006; Traulsen and Nowak, 2006; Taylor et al., 2007; Allen et al., 2013; Simon et al., 2013; Allen and Nowak, 2014; Débarre et al., 2014). However, this effect is sensitive to the details of the evolutionary process: for some models, spatial or group structure can have no effect (Taylor, 1992; Wilson et al., 1992; Ohtsuki et al., 2006; Nowak et al., 2010b) or even a negative effect (Hauert and Doebeli, 2004) on cooperation.

The evolution of cooperation and other social behaviors can be studied mathematically using evolutionary game theory (Maynard Smith and Price, 1973; Maynard Smith, 1982; Hofbauer and Sigmund, 1988, 1998; Weibull, 1997; Nowak and Sigmund, 2004; Nowak, 2006a; Broom and Rychtar, 2013). Social behaviors are represented as strategies, and the fitness consequences of an interaction are quantified as payoffs to each participant. First formulated for large, well-mixed populations (Maynard Smith and Price, 1973), evolutionary game theory has since been extended to populations structured in various ways (Nowak et al., 2010a), including by finite population size (Nowak et al., 2004; Taylor et al., 2004; Imhof and Nowak, 2006), by space (Nowak and May, 1992; Durrett and Levin, 1994; Killingback and Doebeli, 1996; Ohtsuki et al., 2006; Korolev and Nelson, 2011; Chen, 2013; Allen and Nowak, 2014; Débarre et al., 2014; Rand et al., 2014), by groups (Traulsen and Nowak, 2006; Simon et al., 2013), and by social sets (Tarnita et al., 2009a).

Inclusive fitness theory (Hamilton, 1964; Rousset and Billiard, 2000; Wakano et al., 2013; Lehmann and Rousset, 2014) is another approach to studying the evolution of social behavior. In this approach, each individual's fitness (expected number of viable offspring) is expressed as a sum of portions of fitness due to itself and each other individual. An individual's inclusive fitness is then defined as a weighted sum of fitness portions bestowed on self and others, where the weights represent relatedness to the recipient.

Inclusive fitness theory is regarded by its proponents as a general and powerful framework for understanding the evolution of cooperation. However, Nowak et al. (2010b), building on earlier critiques by Cavalli-Sforza and Feldman (1978), Uyenoyama and Feldman (1982), and Matessi and Karlin (1984), showed that fitness is not generally equal to a sum of portions due to separate individuals, and thus the quantity of inclusive fitness is only well-defined in special cases. Some proponents of inclusive fitness theory responded (Abbot et al., 2011; Gardner et al., 2011) that such portions of fitness can always be identified using linear regression (Hamilton, 1970; Queller, 1992; Frank, 1998; see also Birch, 2014). Yet Allen et al. (2013b) showed that this regression method relies on invalid use of statistical inference tools and leads to false conclusions.

A different response was given by Bourke (2011), who acknowledges that calculating inclusive fitness is a technically limited approach to studying social evolution. Bourke argues nonetheless that the more general and powerful methods used in evolutionary game theory and population genetics are still “inclusive fitness approaches”, in that they include the effects of interaction between co-bearers of genes affecting social behavior. We agree that all such effects are accounted for in these mathematically exact methods. However, we find it misleading to refer to these methods as “inclusive fitness approaches”, since the re-assignment of fitness effects from recipient to actor—central to the concept of inclusive fitness—is generally impossible and always unnecessary in applying them.

Given the controversy surrounding inclusive fitness theory, it is worth asking how the consequences of family structure might be investigated using the tools of evolutionary game theory. An important step was provided by Grafen (1979), who developed a deterministic, infinite-population model of evolutionary game dynamics

with a parameter r (sometimes called “relatedness”) quantifying assortment between like types. A fraction r of one's interaction partners guaranteed to be of one's same type, while the remainder are drawn from the population at large. We call this model “ r -replicator dynamics”, because it generalizes replicator dynamics (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1988, 1998) to include assortment. The r -replicator dynamics and variations thereof have been applied to a wide variety of questions in evolutionary dynamics (Eshel and Cavalli-Sforza, 1982; Bergstrom, 2003; Jansen and van Baalen, 2006; Taylor and Nowak, 2006; van Veelen et al., 2012; Alger and Weibull, 2013; Garcia and van Veelen, 2014).

Here we propose a simple model to investigate how family structure affects the evolution of social behavior in a population of finite size. We consider a Wright–Fisher process in which each adult produces a large number of juveniles. Survival of juveniles is determined by their social interactions, which are represented as a game. A fraction r of a juvenile's interaction partners are siblings, and the rest are drawn from the overall juvenile population. Our model extends Grafen's (1979) r -replicator dynamics to populations of finite size.

We derive exact conditions for a strategy to be favored under weak selection. We first obtain results for arbitrary games, and then restrict attention to a subset of games that describe cooperation and defection in social dilemmas. Interestingly, the effect of sibling assortment on the evolution of cooperation depends on the nature of the social dilemma. For the Prisoner's Dilemma and other stringent social dilemmas, cooperation is increasingly favored with r . But for relaxed social dilemmas, sibling assortment can have a negative or even nonmonotonic effect on cooperation.

These results are obtained using straightforward methods based on the probabilities of gene frequency change. In order to connect our results to the literature on inclusive fitness theory, we also attempt to analyze our model using inclusive fitness methods. We find that inclusive fitness is not a well-defined quantity for a general 2×2 payoff matrix, because the contributions that individuals make to each others' fitness cannot be distinguished in a meaningful way. Remarkably, even the linear regression method that is claimed to be “as general as the genetical theory of natural selection itself” (Abbot et al., 2011) fails for this model, because the costs and benefits turn out to be underdetermined. Inclusive fitness is only well-defined for games that satisfy equal gains from switching (Nowak and Sigmund, 1990), but in this case it provides less information than our straightforward analysis based on gene frequencies.

2. Model

Our model is a finite-population analogue of the r -replicator dynamics, and can also be described as a Wright–Fisher game process (Imhof and Nowak, 2006) with assortative interactions among siblings. We consider a population of N haploid adults, each having one of the two competing genotypes, A and B. Reproduction is asexual. A generation consists of three phases:

1. *Proliferation*: Each adult produces a large number $n \gg 1$ of juveniles, so that each parent contributes a fraction $1/N$ of the juvenile population. Juveniles inherit their parent's genotype.
2. *Interaction*: Each juvenile interacts with a large number of others according to the matrix game

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \quad (1)$$

A fraction r of one's interaction partners are drawn from one's siblings, while the remaining fraction $1 - r$ are drawn uniformly from the general population (both siblings and nonsiblings).

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