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Modes of migration and multilevel selection in evolutionary multiplayer games

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HIGHLIGHTS

- We investigate four different modes of migration between groups.
- For each mode we identify multiplayer games favoring the evolution of cooperation.
- The number of games promoting the evolution of cooperation increases as individuals coordinate their migration behavior.
- Weak altruism can evolve via any mode of migration.
- Strong altruism evolves only under coordinated migration modes.

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ABSTRACT

The evolution of cooperation in group-structured populations has received much attention, but little is known about the effects of different modes of migration of individuals between groups. Here, we have incorporated four different modes of migration that differ in the degree of coordination among the individuals. For each mode of migration, we identify the set of multiplayer games in which the cooperative strategy has higher fixation probability than defection. The comparison shows that the set of games under which cooperation may evolve generally expands depending upon the degree of coordination among the migrating individuals. Weak altruism can evolve under all modes of individual migration, provided that the benefit to cost ratio is high enough. Strong altruism, however, evolves only if the mode of migration involves coordination of individual actions. Depending upon the migration frequency and degree of coordination among individuals, conditions that allow selection to work at the level of groups can be established.

1. Introduction

Cooperation can be defined as “a joint action for mutual benefit” (Dugatkin and Mesterton-Gibbons, 1992; Mesterton-Gibbons and Dugatkin, 1992; Clements and Stephens, 1995; Stephens and Anderson, 1997). Participation in a cooperative act is generally costly to cooperators (Hamilton, 1963; Axelrod and Hamilton, 1981; Clements and Stephens, 1995). Therefore, cooperators have lower fitness than non-cooperators (defectors) and, thus, should be eliminated by natural selection. Nevertheless, cooperation is widespread in nature (Crespi, 2001; Porat and Chadwick-Furman, 2004; Wingreen and Levin, 2006). How cooperation evolves and is maintained in the face of selfishness has been the subject of intensive investigation (Hamilton, 1963; Wilson, 1975; Axelrod and Hamilton, 1981; Nowak, 2006b; van Veelen, 2009).

In a group-structured population, members of cooperative groups have a selective advantage over the members of non-cooperative groups. This advantage can make the evolution of cooperation possible (Hamilton, 1964; Wilson, 1975; Traulsen and Nowak, 2006; Nowak, 2006b). The essential idea is that population structure channels cooperation preferentially to other cooperators (Fletcher et al., 2006; Fletcher and Doebeli, 2009). Wilson and Wilson (2007) formulated this as: “Selfishness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary.” However, the interplay between these effects is important because it determines whether cooperation will evolve.

Group structure by itself does not provide an advantage to cooperation (Godfrey-Smith, 2009) – indeed within groups, selfish types have an advantage over cooperating types (Wilson, 1975).

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For cooperating types to be maintained, groups must participate in some kind of birth and death process. Individuals arising within one group must have an opportunity to become a member of another group. There are many ways by which this may occur. For instance, in standard trait group models (Wilson, 1975; Avilés, 2002; Garcia and de Monte, 2013), individuals within groups are released into a global pool and then randomly form new groups. Alternatively groups may fragment (Traulsen and Nowak, 2006). A further possibility is that individuals from one group may migrate to another (Christiansen, 1975; Kelly, 1992; Hauert and Imhof, 2012; Hauert et al., 2014). Via the process of migration, groups themselves do not reproduce in a conventional sense, but the effects are parallel.

In this study we consider models where an individual may become a member of another group by migration between groups. Individuals migrating from one group to another may fixate in the new group, or be eradicated as a consequence of individual-level selection. A defecting individual has a higher probability of fixation in a group of cooperators than does a cooperating individual in a group of defectors, thus individual-level selection favours defectors. However, individuals in groups of cooperators are more productive than in groups of defectors, and therefore groups of cooperators release more migrants than do groups of defectors. Thus, while previous studies have shown that migration makes cooperation more difficult to evolve (because it brings about the mixing of groups (Traulsen and Nowak, 2006), recent work shows that rare migration can favor cooperation (Hauert et al., 2014). Here, we consider a range of modes by which migration might occur and describe ensuing effects on the evolution of cooperation.

Migration can be implemented in multiple ways: individuals may migrate individually, or in clumps; subsequent migrations may or may not be influenced by previous ones; migration may be triggered by signals perceived by individuals, or may be influenced by the group. In this study we compare different modes of migration. For each mode, we identify the games in which cooperation is evolutionarily successful, i.e., where selection at the group level is strong enough to overcome selection at the individual level. The comparison between modes of migration shows that the set of games in which cooperation evolves generally expands with increasing degrees of coordination surrounding the migration process.

2. Evolutionary dynamics within a single group

We make the assumption that individuals live in a population with a fixed number of groups. The interactions between all individuals within a group are determined by a multiplayer game. The payoff of each individual depends on its strategy and the composition of the group. Each individual can be either a cooperator (C) or a defector (D). The size of the game is equal to group size. Thus, all players sharing the same strategy within a group have the same payoff. More specifically, the payoff of a cooperator in a group with i cooperators and $n-i$ defectors is a_i, and the payoff of a defector in a group with i cooperators and $n-i$ defectors is b_i. Thus, a game is completely determined by two sequences, $a_1, \ldots, a_n$, and $b_0, \ldots, b_{n-1}$ (Kerr et al., 2004; Gokhale and Traulsen, 2010).

We use an exponential function to map payoff to fitness. The fitnesses of cooperators and defectors in a group with i cooperators are therefore e^{wa_i} and e^{wb_i}, respectively (Traulsen et al., 2008). Here, w measures the intensity of selection. For $w=0$, selection is neutral. For $w \ll 1$, the fitness is approximately linear in payoffs. For large w, small differences in payoffs lead to large fitness differences.

The evolutionary dynamics are governed by a Moran process. At each time step a single individual in the population is chosen for reproduction with probability proportional to fitness (Moran, 1953; Nowak et al., 2004). This chosen individual produces identical offspring, replacing a randomly chosen individual. Thus, population size is kept constant. For such a process, the probability for a single cooperator to take over the whole population, ϕ_C, can be calculated exactly, as well as the probability of a single defector taking over the whole population, ϕ_D (Goel and Richter-Dyn, 1974; Traulsen et al., 2009). These fixation probabilities form the basis of our measure of success for each strategy.

In order to compare the evolutionary success of the two strategies C and D, we examine whether $\phi_C > \phi_D$. Thus, the value of ϕ_C/ϕ_D determines which strategy is more common. For a ratio greater than 1, cooperation is favoured over defection. If the ratio is less than 1, defection is favoured. The fixation probabilities of cooperators and defectors in the Moran process with exponential mapping are (Karlin and Taylor, 1975; Nowak et al., 2004; Traulsen et al., 2008)

$$\phi_C = \frac{1}{1+\sum_{j=1}^{n-1}\prod_{i=1}^{j} e^{w(b_i-a_i)}} \tag{1}$$

$$\phi_D = \frac{1}{1+\sum_{j=1}^{n-1}\prod_{i=1}^{j} e^{w(a_{n-i}-b_{n-i})}}. \tag{2}$$

The ratio of the fixation probabilities is given by (Nowak, 2006a)

$$\frac{\phi_C}{\phi_D} = \prod_{i=1}^{n-1}\frac{e^{wa_i}}{e^{wb_i}} = e^{w\sum_{i=1}^{n-1}(a_i-b_i)}. \tag{3}$$

Whether this ratio is greater than 1 (i.e. cooperators are favoured) depends solely on the sign of

$$\Lambda_0 = \sum_{i=1}^{n-1}(a_i-b_i). \tag{4}$$

This is a generalization of the classic result of risk dominance to multiplayer games (Kandori et al., 1993; Nowak et al., 2004; Fudenberg et al., 2006; Antal et al., 2009; Kurokawa and Ihara, 2009; Gokhale and Traulsen, 2014). For a positive Λ_0, cooperation is favoured in terms of the fixation probability, while a negative Λ_0 means that defectors are selected. We will use such Λ values for comparing the different migration modes.

3. Migration modes

We now extend this analysis to multiple groups, and include migration between groups (see Fig. 1). Consider m different groups, each with a fixed group size of n. We discuss several different modes of migration that individuals can use to move between groups.

The rate of migration between groups is assumed to be very small compared to the rate of fixation of a strategy within a group. This implies that migration events typically occur only when groups are homogeneous (Traulsen and Nowak, 2006; Traulsen et al., 2008). Under this time-scale separation, fixation events in the whole population occur in two stages: first a strategy fixes inside a group – with probability ϕ_C (ϕ_D) for cooperators (defectors) – and then in the whole population – with probability Φ_C (Φ_D) for groups of cooperators (defectors).

We use Eqs. (1) and (2) to compute ϕ_C and ϕ_D at the individual level. At the group level, the fixation probabilities Φ_C and Φ_D depend on the mode of migration. Expressions for these probabilities are generally simpler than for the probabilities at the individual level due to the fact that all individuals within a group