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Cooperation and punishment in community-structured populations with migration

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HIGHLIGHTS

- For weak local selection, conflict between groups leading to full group extinction can sustain cooperation for very large group sizes.
- Migration proportional to fitness is methodologically simpler than migration between groups of variable size.
- Fitness-based migration as a model of individual competition shows evolutionary outcomes similar to explicit group conflict.

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ABSTRACT

The stable presence of punishing strategies in various cooperative species is a persistent puzzle in the study of the evolution of cooperation. To investigate the effect of group competition, we study the evolutionary dynamics of the Public Goods Game with punishment in a metapopulation that consists of separate communities. In addition to (a) well-mixed non-interacting communities, we model three distinct types of interaction between communities, (b) Migration independent of fitness; (c) Competition between whole communities, where entire communities replace each other depending on average fitness; (d) Migration where the probability of an offspring replacing an individual in another community depends on fitness. We use stochastic simulations to study the long-run frequencies of strategies with these interactions, subject to high mutation and migration rates. In cases (a) and (b), the transition between cooperation/punishment and defection regimes occurs for similar parameter values; with migration (b), the transitions are steeper due to higher total mixing. Fitness-based migration (d) by contrast can help support cooperation, changing the locations of transitions, but while group selection (c) does stabilise cooperation over much of the parameter space, fitness-based migration (d) acts as a proxy for group selection only in a smaller region.

1. Introduction

The *Public Goods Game* is a well-studied game-theoretical model, which is frequently used to illuminate the social dilemma known as the *Tragedy of the Commons* (Hardin, 1968). The *Linear Public Goods Game with peer punishment* (PGG/P) considered here is a symmetric game, involving N players. All of the N agents playing the PGG choose simultaneously to either contribute a fixed cost c, which they invest into sustaining a public resource, or to abstain from investing. Abstaining players are referred to as *defectors* (D). The investments into the public venture are then scaled up by a linear factor $1<r<N$ and split between all players. In addition to merely contributing, *i.e.* following the *cooperator* (C) strategy, the PGG/P allows contributors to punish defectors. After the first stage payoff has been declared as described above, each *punisher* (*P*) pays a punishment cost proportional to the number of defectors (normalised as γ/N per defector, so that the maximal punishment cost is independent of the population size), in order to inflict a fine β/N each on every defector. The individual payoffs for defectors (π_D), cooperators (π_C) and punishers (π_P) from the PGG/P with n_s players following strategy s respectively is therefore given by:

$$\pi_D = \Pi - \beta \frac{n_P}{N} \tag{1}$$

$$\pi_C = \Pi - c \tag{2}$$

$$\pi_P = \Pi - c - \gamma \frac{n_D}{N} \tag{3}$$

where $\Pi = rc\frac{n_C+n_P}{N}$ is the individual's share in the public good. For well-mixed populations, the evolutionary dynamics of this model has

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been extensively studied in the past, including with a focus on the influence of mutations (García and Traulsen, 2012; Hauser et al., 2014).

Under low mutation rates, punishment cannot increase cooperation levels in the long run. Defectors are very unlikely to fixate in a pure punisher population. Cooperators however behave as second-level free riders, because the profit from the second-order public good, the punishment, provided by the punishers, without contributing themselves. They are thus fitter than punishers in the presence of defectors. In the absence of defectors, genetic drift still leads to a significant number of transitions towards pure cooperation. Such a population can be easily invaded by defectors, and is itself safe against invasion by cooperators and punishers. Even with punishment, cooperation can therefore not prevail.

This is different for high mutation rates. This effect has been previously observed by Traulsen et al. (2009), who showed that cooperation and punishment can dominate defection even in well-mixed populations, when mutation rates are high. For comparison with results below, we show the mean strategy frequencies for the PGG/P in well-mixed populations with high mutation, depending on the two parameters c and γ, in Fig. 1. For some range of these parameter values, cooperative strategies outcompete defectors even though the population is well-mixed. On the other hand, when punishment is deactivated, by setting $\beta = \gamma = 0$, cooperation cannot prevail under any circumstance.

It is however well-known (Nowak et al., 2010a; Perc et al., 2013; Szabó and Fáth, 2007; Perc and Szolnoki, 2010, 2012; Helbing et al., 2010) that the structure of an evolving population has great influence on the evolutionary dynamics of a model. Cooperation, where other individuals gain a benefit at a cost to a cooperator, is known to be able to evolve if the structure of the population ensures that those benefits are mostly received by other cooperators, rather than being distributed uniformly.

This effect is not restricted to populations on lattices or arbitrary graphs, but also apparent in island- or community-structured populations (Wang et al., 2011). Similar population structures have been considered in evolutionary modeling for a long time, starting with Wright's considerations of migration (Wright, 1931). These models have become known under a variety of names, such as deme-structured populations (Wilson, 1975), patch-structured populations (Powers and Lehmann, 2013), finite island dispersal models (Powers and Lehmann, 2013), or viscous populations (Rodrigues and Gardner, 2013).

In this paper, we study effects of group selection on the evolutionary dynamics of the linear PGG/P. We construct a metapopulation that consists of separate communities. Agents play the public goods game and produce offspring in their local community according to a Moran-like process with a Fermi updating rule (Kaiping et al., 2014; Wu et al., 2011; Altrock and Traulsen, 2009; Szabó and THoke, 1998; Szolnoki et al., 2009), but have a small chance to produce offspring in a different community. The chances of successfully producing offspring into a different community will depend on the specific model of interaction. We investigate how these different interactions between communities affect the long-term behaviour of the system.

Lehmann et al. (2007) have proven analytical results on the effect of punishment in community-structured populations with negligible mutation. In their study, the offspring of a population of punishers and defectors will contain equal proportions of cooperators and punishing defectors, or cooperators will be entirely absent from the system in the absence of recombination. For this case, they have shown that punishment supports the evolution of cooperation only in cases where it is already supported by the population structure in the absence of punishment. In this paper, we instead consider the case of significant mutation rates, and we focus on a model without recombination, but with cooperators.

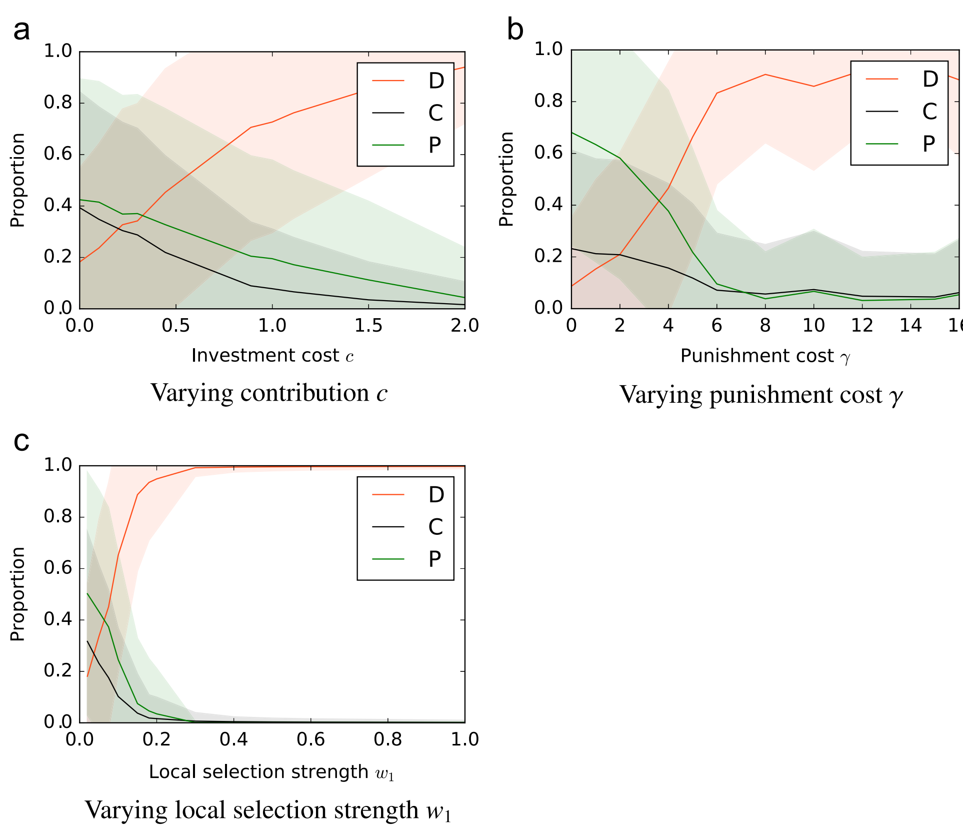

Fig. 1. Frequencies of strategies in the equilibrium state of the PGG/P in a well-mixed population, under variation of different parameters. All other parameter are as given in Table 1. Solid lines show the mean of the frequency in the long-time limit, the shaded area denotes the $\pm 1\sigma$ band around it.