



Group-level events are catalysts in the evolution of cooperation



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HIGHLIGHTS

- Hunter-gatherer model with births, deaths, migration, fission, extinction, intra-group assortment.
- Fission/extinction speeds up the evolution of cooperation.
- Fission/extinction allows cooperation to thrive under unfavorable conditions.
- Fission/extinction can counter the effects of moderate levels of migration.

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ABSTRACT

Group-level events, like fission and extinction, catalyze the evolution of cooperation in group-structured populations by creating new paths from uncooperative population states to more cooperative states. Group-level events allow cooperation to thrive under unfavorable conditions such as low intra-group assortment and moderate rates of migration, and can greatly speed up the evolution of cooperation when conditions are more favorable. The time-dependent effects of fission and extinction events are studied and illustrated here using a PDE model of a group-structured population based loosely on populations of hunter-gatherer tribes. By solving the PDE numerically we can compare models with and without group-level events, and explicitly calculate quantities associated with dynamics, like how long it takes a small population of cooperators to become a majority, as well as equilibrium population densities.

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1. Introduction

In mathematical models of evolutionary processes, cooperation is characterized by behaviors that are detrimental to the individual, but advantageous to the individual's social partners, e.g. Nowak (2006). Here, we will call individuals that exhibit cooperative behaviors *cooperators*, and those that do not will be called *defectors*. Cooperative behaviors are very common in the natural world, but in general their evolution is more difficult to explain than the evolution of traits or behaviors that more directly benefit the individual, Darwin (1859), Darwin (1871), Hamilton (1964), Dawkins (1976), Maynard Smith and Szathmary (1997), Sober and Wilson (1998), Okasha (2006), Nowak (2006), Fletcher and Doebeli (2009), Tarnita et al. (2013). Mathematical explanations of the evolution of cooperation based on kin selection theory

date back to Fisher (1930), Haldane (1932), Hamilton (1964), and Price (1972), but the basic ideas were anticipated much earlier, e.g. Darwin (1859), who sought to explain the existence of sterile castes of social insect. Mathematical explanations of the evolution of cooperation based on group selection theory date back to Maynard-Smith (1964), Maynard Smith (1976), Gilpin (1975) and Wilson (1975a), but the basic ideas here also date back to Darwin (1871), who wondered if competition between tribes of humans in the past may explain modern human cooperation. Since the 1960s, both kin selection theory and group selection theory have gone through a number of changes and generalizations, Wynne-Edwards (1962), Williams (1966), Maynard-Smith (1964), Maynard Smith (1976), Price (1972), Wilson (1975b), Wilson (1975a), Dawkins (1976), Damuth and Heisler (1988), Goodnight et al. (1992), Sober and Wilson (1998), Wilson and Wilson (2007), Gardner et al. (2011), Frank (2012), Frank (2013), Simon et al. (2013). Here we take Prod. Type: FLPA group selection approach to the evolution of cooperation, and in particular, we use the definitions of group selection and related concepts proposed and defended in Simon

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et al. (2013), which can be summarized for our current purposes as follows:

Definition 1. Group-level events include all biological events that change the number of groups in a population.¹ A trait evolves by group selection in a model of a group-structured population if it establishes itself when group-level events are present in the model, and does not establish itself when they are absent. In other words, an individual-level trait (like cooperation) evolves by group selection in a model if the group-level events are *decisive*, in the sense that when the other model parameters are held fixed, the trait evolves if and only if the group-level events occur frequently enough.

A trait that does not (strictly) evolve by group selection may still be assisted by group-level events, for example if it establishes itself more quickly and/or more completely when group-level events are present in the model than when they are absent.

The primary reason biologists study group selection is the theoretical possibility that a trait that is disadvantageous for individuals within their groups, can nevertheless thrive in the population because groups containing more individuals with the trait (or a larger fraction with the trait) are endowed with some kind of advantage over other groups. The nature and strength of this group-level advantage, and its cause, is not the same in every model. For example, in many models, abundance of the trait in a group is correlated with a faster group growth rate (i.e., higher MLS1 fitness, Okasha, 2006), which can lead to an increase of the trait in the population. This is the kind of group selection that is often said to be mathematically equivalent to kin selection, e.g. Gardner et al. (2011). However, this is *not* the kind of group selection we are talking about here, since group-level events in those models may not be decisive, or may be absent altogether. A faster group growth rate from an abundance of a trait is neither necessary nor sufficient for group selection to occur. (See Simon et al., 2013 for an example of group selection where groups with more of a cooperative trait actually grow slower). The kind of group selection we are talking about here occurs when groups gain their advantage directly or indirectly from the effects of group-level events, e.g., a lower extinction rate for groups with an abundance of the trait. There is no ambiguity in this definition because the advantage can be measured by solving the model with and without the group-level events. Maynard Smith (1976), described a similar kind of group selection in words, but his models did not include realistic group-birth events, like fission. Since fission events create much of the group-level diversity that the group extinction events select on, his models underestimated the strength of group selection.

The analysis here is not the first in the literature to study the effects of fission and extinction on group-structured populations mathematically. Previous work using continuous-time Markov chains and/or PDE models includes Simon (2010, 2014), Simon and Nielsen (2012), Simon et al. (2012, 2013), Luo (2013), van Veelen et al. (2014). Previous to that body of work, Traulsen and Nowak (2006), and Lehmann et al. (2007), studied a group-structured population of cooperators and defectors with the same biological events considered here (births, deaths, migration, fission, extinction), and found conditions for cooperators to be more likely to

fixate than defectors, starting with a single mutant. Traulsen and Nowak used a multi-level selection approach to the problem (nested Moran processes). Lehmann, et al. used a kin selection approach to the same basic model, showing that at least some aspects of the model could be studied either way. Both papers found that group-level events promote cooperation, in the sense that without them, defectors are always more likely to fixate. The analytical results in both papers are restricted to limiting versions of the basic model, where the fission, extinction, and migration rates converge to zero, and where there is weak selection between cooperators and defectors within the groups. (Traulsen and Nowak obtain results when fission, extinction, and migration rates are nonzero by simulation, but they assume weak selection throughout.) In this paper, and with PDE models in general, there are no restrictions on any of the model parameters, as long as the resulting rate functions are nonnegative and differentiable in the population variables. In particular, there is no need to assume constant populations. Thus, the scope of the PDE model is much larger. However, the most significant differences between the analyses in Traulsen and Nowak, and Lehmann et al. and the present work have to do with dynamics. Those analyses are insensitive to the time scales and trajectories of the evolutionary processes, and therefore cannot address the main questions posed here, which involve rates of evolutionary change. Furthermore, fixation is not the criteria for evolutionary success here. In fact, fixation does not occur in general in PDE models of group-structured populations, Simon (2010), Simon et al. (2013), Luo (2013). When the rates of group-level events are positive, the equilibrium typically is a smooth density function corresponding to a diverse population of groups of varying sizes and compositions. Diversity in equilibrium has been observed before in models of cooperators and defectors, e.g. Doebeil et al. (2004), Archetti and Scheuring (2010). Of course, fixation theoretically occurs in finite time in any finite population, since the population state space is finite and fixations are the only absorbing states. But the PDE models suggest that the time to fixation may be very large in group-structured populations with group-level events, especially when populations (of groups and individuals) are large, so fixation probabilities may not always be the appropriate way to characterize the evolution of cooperation in group-structured populations.

Likewise, the static analysis of a group-structured model with fission events (referred to as budding) in Gardner and West (2006) is not sensitive to the kinds of dynamical effects and equilibrium outcomes found here, although it does find that budding benefits cooperation. Theoretically, it might be possible to obtain equilibrium population densities numerically for our PDE models by a static analysis (by setting the time derivative to zero, and solving the resulting equation), but this has not yet been demonstrated, and even if equilibrium densities can be found this way, important questions concerning evolutionary rates and trajectories would remain unanswered.

Of course, group selection is not the whole story in the evolution of cooperation. The definition of group selection we use here does not preclude the possibility that other factors are decisive (or assist) in the evolution as well. The evolution of cooperation can be the net result of multiple factors. In particular, it is well known that if cooperators (defectors) are more likely to interact socially with other cooperators (defectors) than pure chance would allow, then cooperation typically evolves more easily in the model. This is one of the basic insights of kin selection theory, Hamilton (1964). Thus, the level of assortment within the groups (which quantifies the social interaction asymmetry in our model) may also be decisive. Comparisons between group selection and kin selection, as explanations of the evolution of cooperation in a given model, are (or should be) about the relative efficacy of model variables like the level of assortment within the

¹ Some events that cause abrupt changes in the state of the population are also group-level events, even if the number of groups does not change. For example, an event where a group dies and another is born, simultaneously, is a group-level event. See Simon et al. (2013) for formal definitions of group-level and individual-level events.

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