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Long-Time Behavior of a PDE Replicator Equation for Multilevel Selection in Group-Structured Populations

In many biological systems, natural selection acts simultaneously on multiple levels of organization. This scenario typically presents an evolutionary conflict between the incentive of individuals to cheat and the collective incentive to establish cooperation within a group. Generalizing previous work on multilevel selection in evolutionary game theory, we consider a hyperbolic PDE model of a group-structured population, in which members within a single group compete with each other for individual-level replication; while the group also competes against other groups for group-level replication. We derive a threshold level of the relative strength of between-group competition such that defectors take over the population below the threshold while cooperation persists in the long-time population above the threshold. Under stronger assumptions on the initial distribution of group compositions, we further prove that the population converges to a steady state density supporting cooperation for between-group selection strength above the threshold. We further establish long-time bounds on the time-average of the collective payoff of the population, showing that the long-run population cannot outperform the payoff of a full-cooperator group even in the limit of infinitely-strong between-group competition. When the group replication rate is maximized by an intermediate level of within-group cooperation, individual-level selection casts a long shadow on the dynamics of multilevel selection: no level of between-group competition can erase the effects of the individual incentive to defect. We further extend our model to study the case of multiple types of groups, showing how the games that groups play can coevolve with the level of cooperation.