Numerical Solutions and Animations of Group Selection Dynamics

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ABSTRACT

Question: What is the best way to illustrate the dynamical process of group selection, and demonstrate its long-term characteristics?

Approach: Numerically solve the dynamical equations for general two-level population processes, and then animate the results.

Mathematical Methods: Numerical PDE, Numerical ODE, Stochastic Simulation.

Key Assumptions: Group selection is properly characterized in terms of the long-term behavior of two-level population processes.

Main Results: The dynamical process of group selection can be seen clearly in three different kinds of animations of the dynamical equations. The three kinds of animations, corresponding to different scalings of the basic model, highlight different aspects of the phenomenon. Group selection appears to be a potent evolutionary force under a variety of conditions, contrary to common belief.

keywords: multi-level selection, group fissioning, group extinction, evolutionary birth-death process, population dynamics.

1 Introduction

Under the right conditions, group selection is a phenomenon that can happen, over time, in a two-level population process. A two-level population process is one where groups of individuals compete in an environment containing other groups of individuals, and the individuals within each group compete against each other as well. In Simon, Fletcher & Doebeli (2012b), a simple mathematical definition of group selection is given in terms of the long-term behavior of the solutions of the dynamical equations for two-level population processes. The dynamical equations are derived from first principles (e.g., birth and death rates at the individual and group levels), Simon (2010), so the definition of group selection based on them applies generally to all examples of two-level population processes, subject to a few basic structural conditions, e.g., nonoverlapping groups and a discrete set of individual types. Here, we describe how one obtains numerical solutions for the equations of two-level population dynamics, and we illustrate the solutions by animating them. From the animations it is easy to see how, and under what conditions, group selection occurs.

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The most basic model of two-level population processes considered here is purely stochastic; a continuous-time Markov chain to be precise. The state space for the continuous-time Markov chain is rather complicated, so the only practical way to analyze it exactly is by simulation. We therefore refer to the Markovian model as our simulation model. By taking a certain limit of simulation models (as the populations of individuals within the groups tends to infinity) a process emerges that is partly deterministic and partly stochastic, Puhalskii and Simon (2012). We call this the hybrid model, because the solution involves both a numerical solution of a certain system of ODE's, and a simulation. By taking an additional limit on the simulation model (this time as the number of groups tends to infinity) a process emerges that is completely deterministic. We call this the PDE model because the the resulting dynamical equation is a first order hyperbolic PDE, Simon (2010).

Solutions of the three models highlight different aspects of the evolutionary trajectories and equilibrium configurations of two-level population process. The simulation and hybrid solutions highlight the life histories of individual groups from the moment they are "born" (as a fissioned piece of a "parent" group), to the moment they "die" (by fissioning into pieces, or by extinction). In animations of the simulation solution, the irregular within-group population fluctuations sometimes makes it hard to follow individual groups as they change in time. In the hybrid model, the within-group population dynamics are deterministic (the solutions of certain ODE's), while the group-level events remain stochastic. By smoothing out the within-group population dynamics in the hybrid model, the animations are much easier to follow. The PDE model smooths out fluctuations at both levels, thereby highlighting the "average" evolutionary path that leads from the initial condition to an equilibrium. The individual groups cannot be seen in the animations of the PDE solution, since the population of groups is represented by a smooth density function. In equilibrium, the PDE solution stops changing, so the interesting part of the animation is relatively short in duration. The simulation and hybrid solutions, by contrast, continue to "move" indefinitely, although their basic configuration eventually stops changing, i.e., they reach a statistical equilibrium. Thus, the simulation and hybrid solutions are particularly useful for illustrating how equilibrium configurations remain stable, and the PDE solution is particularly useful for illustrating how the environment transforms from the initial configuration to the equilibrium. In many examples, all three models can be solved numerically, and much can be learned by studying them together, as we will show.

To keep things as simple as possible here, we will restrict the kinds of events in the models to individual-level births and deaths, and group-level fissioning and extinction; and consider only two individual-types, which we will call Cooperators and Defectors. These assumptions suffice for interesting and realistic two-level evolutionary processes. In Simon (2010) and Simon, et.al. (2012a,b), other events like individual-level migration, and group-level fusion and dispersion are allowed in the models, and $k \geq 2$ individual types are allowed. In the next section we describe the simulation, hybrid, and PDE models of two-level population dynamics in more detail, and explain how they are mathematically related, and how they are numerically solved. In section 3 we present some animations (links to YouTube videos) of the three solution techniques applied to a variety of examples of the evolution of cooperation, and in section 4 we summarize the results and place them in context with current thought on group selection.

2   Three related models and their numerical solutions

In this section we describe three closely related models of two-level population dynamics, and explain how they can be solved numerically. The basic model is a continuous-time Markov chain, and the other two models are derived from it by taking certain limits.

2.1 The simulation model

Our continuous-time Markov chain model of two-level population dynamics is specified by the (stochastic) rates that the various individual-level and group-level events occur at, as functions of the state of the environment, and a rule that specifies how the state changes when an event occurs. Thus, the modeler chooses the form of

1. $B_c(x,y)$ and $B_d(x,y)$, the birth rates of Cooperators and Defectors in an (x,y)-group.

2. $D_c(x,y)$ and $D_d(x,y)$, the death rates of Cooperators and Defectors in an (x,y)-group.

3. $F_\theta(x,y)$, the rate that (x,y)-groups fission when the state of the environment is θ.

4. $f((x,y),(u,v))$, the expected number of (u,v)-groups resulting from the fissioning of an (x,y)-group (referred to as the "fissioning density").

5. $E_\theta(x,y)$, the rate that (x,y)-groups die of extinction when the state of the environment is θ.

The dynamical state of the environment, $\theta_t(x,y)$, $t \geq 0$, changes whenever a birth or death occurs within a group, or a group fissions or dies of extinction. When a birth or death occurs in an (x,y)-group at time t, the state of that group changes from (x,y) to one of $(x \pm 1, y \pm 1)$. The state of the environment is updated by decreasing $\theta_t(x,y)$ by one and increasing the appropriate $\theta_t(x \pm 1, y \pm 1)$ by one. When an (x,y)-group fissions, the offspring group-types, (u,v) and $(x-u,y-v)$, are determined by sampling randomly from the fissioning density. The state of the environment is updated by decreasing $\theta_t(x,y)$ by one, and increasing $\theta_t(u,v)$ and $\theta_t(x-u,y-v)$ by one. If an (x,y)-group dies from extinction at time t then, $\theta_t(x,y)$ is decreased by one. There are standard techniques for determining the timing of the events in a simulation of a continuous-time Markov chain, that exploit special properties of exponential distributions, e.g., Gillespie (1977).

Very often simulations are used to estimate probabilities or expected values associated with a model by repeating the simulation many times and computing an average, i.e., Monte-Carlo simulation. Our simulation can be easily modified for this purpose, however, our goal here is to gain insights into the stochastic process itself, so we generate long "sample paths" from the simulation, and then animate them. From a practical perspective, simulation is a very attractive approach to studying two-level population dynamics, and for models with small populations it is the most accurate solution technique. However, simulation can be computationally expensive if the size and/or number of groups in the model are too large. The hybrid solution is always faster, and sometimes the PDE solutions may be faster too. Also, the sample paths from the simulation are rather irregular due to the random timings of all the events, so animations of the hybrid and PDE solutions are easier to follow.

2.2 A hybrid simulation/ODE method

In Puhalskii and Simon (2012) it is shown that as the population of individuals within a group tends to infinity, the (properly scaled) population dynamics converges to the solution of a certain system of ODE's. Of course, the solutions of the differential equations can be used to approximate within-group population dynamics whether or not the populations are large. When populations are small, the solutions of the differential equations can be thought of as the "average" evolutionary trajectory. The ODE's have the simple form,

$$x' = \alpha_c(x,y) = x(B_c(x,y) - D_c(x,y)) \quad \text{and} \quad y' = \alpha_d(x,y) = y(B_d(x,y) - D_d(x,y)), \quad (1)$$

which are easily solved by standard techniques like Euler's method or Runge-Kutta, Hoffman (2001). Note that the individual-level birth and death rates, interpreted as stochastic rates in the simulation model, are

interpreted as deterministic rate functions in the hybrid model. The states of the groups in the hybrid solution therefore take values in the continuum, $\mathfrak{R}_+^2$, since the evolutionary trajectories are continuous. The number of groups in the hybrid model is always integer valued, though. The only remaining detail to work out for the hybrid model is the fissioning density. In this context (and also for the PDE model), the fissioning density is a "smoothed-out" version of the fissioning density used in the simulation model, i.e., a function satisfying

$$\int\int uf((x,y),(u,v))dvdu = x \qquad \text{and} \qquad \int\int vf((x,y),(u,v))dvdu = y, \qquad (2)$$

so the sum of the pieces equals the whole. The continuous fissioning density for the hybrid model emerges as a limit of the discrete fissioning densities from the simulation model, e.g., a discrete uniform density becomes a continuous uniform density in the limit. In general, no two groups in the environment will be in exactly the same state in the hybrid model.

The within-group population dynamics, governed by (1), abruptly ends when a group fissions or dies. In the hybrid simulation/ODE method, the timing of the group-level events retains its stochastic nature from the simulation model. The hybrid model is solved using the same time step, Δt, that is used to solve the ODE's numerically. In each time step, $[t, t + \Delta t)$, the probability that an (x,y)-group fissions is $F_{\theta_t}(x,y)\Delta t + o(\Delta t)$, and the probability it dies of extinction is $E_{\theta_t}(x,y)\Delta t + o(\Delta t)$, where θ_t is the state of the environment at the beginning of the time step. The time step is chosen small enough so that the solution of the ODE is accurate, and so that $o(\Delta t)$ can be safely ignored in the simulation. The simulation determines which (if any) groups fission or die during the time step, and then the new state of the environment determined by

- If an (x,y)-group does not fission or die during the time interval then it goes to state $(x,y) + (x',y')\Delta t$. (Note, this is Euler's method. Runge-Kutta or any other standard method can also be used.)

- If an (x,y)-group fissions during the time interval, then (u,v) is determined from the fissioning density, and the state of the environment is updated by decreasing $\theta_{t+\Delta t}(x,y)$ by one, and increasing $\theta_{t+\Delta t}(u,v)$ and $\theta_{t+\Delta t}(x-u,y-v)$ by one.

- If an (x,y)-group dies of extinction during the interval, then decrease $\theta_{t+\Delta t}(x,y)$ by one.

The hybrid solution is typically much faster than the simulation solution because the effects of individual-level births and deaths in each time step are replaced by a single deterministic calculation.

2.3 A numerical PDE solution

In Simon (2010), a certain PDE is derived from the simulation model by interpreting population sizes (of groups and individuals within the groups) to be real valued, and interpreting all the stochastic rate functions as deterministic rate functions. The result is a deterministic process, where the dynamical state of the environment is governed by

$$\frac{\partial \theta_t}{\partial t}(x,y) + \frac{\partial(\theta_t \alpha_c)}{\partial x}(x,y) + \frac{\partial(\theta_t \alpha_d)}{\partial y}(x,y) = g_t(x,y), \qquad (3)$$

where $\alpha_c(x,y)$ and $\alpha_d(x,y)$ are the net growth rates of Cooperators and Defectors in an (x,y)-group from (1), and

$$g_t(x,y) = \int\int \theta_t(u,v)F_{\theta_t}(u,v)f((u,v),(x,y))dudv - (E_{\theta_t}(x,y) - F_{\theta_t}(x,y))\theta_t(x,y) \qquad (4)$$

is the difference between the rates (x,y)-groups "appear" at time t due to larger groups fissioning, and the rates they "disappear" due to fissioning and extinction at time t.

Although (3) has no analytic solution, it can be solved numerically. One way to solve the equation numerically starts by truncating $\mathfrak{R}_+^2$ into a finite rectangle, $R = [0, x_{max}] \times [0, y_{max}]$, large enough so that the

fraction of (x, y)-groups outside R is always very small. R is then partitioned into a rectangular grid, where each cell in the grid has size $\Delta x \times \Delta y$. Time is similarly discretized into time steps of duration Δt. The state of the environment at time $t_n = n\Delta t$ is represented by an $m_x \times m_y$ matrix, Θ_n, where $m_x = x_{max}/\Delta x$, $m_y = y_{max}/\Delta y$, i.e., $\Theta_n(i, j)\Delta x \Delta y$, is (approximately) the number of (x, y)-groups in the environment at time t_n, where (x, y) is in the (i, j)-cell. The state is recalculated at time t_{n+1} from the state at time t_n by updating each element of Θ_n based on individual-level changes (from the partial derivative terms) and group-level changes (from the g_t term) that occur in the $n + 1$st time interval. The changes to $\Theta_n(i, j)$ due to individual-level changes is computed in terms of the values in its neighboring cells; and the growth rate functions, α_c and α_d, from (1). The method of "upwind differencing", Hoffman (2001), seems to work well. For the group-level changes, we update $\Theta_n(i, j)$ by adding $g_{t_n}(i\Delta x, j\Delta y)\Delta t$, obtained from a numerical integration of (4).

3 Animations

Properly designed simulations of continuous-time Markov chains are exact, in the sense that the underlying probability space for the simulation is the same as the underlying probability space for the continuous-time Markov chain. And under the weak assumption that the rate-functions, B_c, B_d, D_c, D_d, F_θ, and E_θ, defined in the previous section, are continuous in the variables x and y (or even piecewise continuous), the numerical solutions described in the previous section for the hybrid and PDE models can be made as accurate as the modeler wants, by setting the time steps and grid sizes sufficiently small. There is therefore an enormous range of possible two-level population models that are amenable to mathematical analysis. Our tactic in this section is to choose simple generic forms for the rate functions, and reasonable values for the associated parameters, with the goal of animating "typical" two-level population dynamics.

Our animations will be based on models of two-level population dynamics with the following rate functions. In the absence of mutation, the birth rates in an (x, y)-group are

$$\hat{B}_c(x, y) = \beta + \frac{x}{x+y}b - c, \qquad \text{and} \qquad \hat{B}_d(x, y) = \beta + \frac{x}{x+y}b,$$

i.e., Cooperators and Defectors play a public goods game within their groups, where each cooperator produces a benefit b, shared by all the individuals in the group, at a cost of c to itself. The parameter β is a base birth rate common to both types. Let μ_c be the probability that the offspring of a Cooperator is a Defector, and let μ_d be the probability the offspring of a Defector is a Cooperator. Then the total rates that Cooperators and Defectors are born in an (x, y)-group, including "mutations", are

$$B_c(x, y) = (1 - \mu_c)\hat{B}_c(x, y) + \mu_d \hat{B}_d(x, y) \qquad \text{and} \qquad B_d(x, y) = \mu_c \hat{B}_c(x, y) + (1 - \mu_d)\hat{B}_d(x, y). \qquad (5)$$

The death rates for Cooperators and Defectors in an (x, y)-group are equal, with

$$D_c(x, y) = D_d(x, y) = (x + y)\gamma. \qquad (6)$$

Since the per-individual death rates are proportional to the size of the group, but the per-individual birth rates are bounded, there is an equilibrium group size (depending on the fractions of Cooperators and Defectors in the group) where birth and death rates balance. In particular, in a group that is primarily Cooperators, the equilibrium size is $(\beta + b - c)/\gamma$, and in a group that is primarilly Defectors, the equilibrium size is β/γ. The equilibrium sizes for groups with a mixture of cooperators and defectors will be between those values.

The fissioning rate for an (x, y)-group in our examples is

$$F_\theta(x, y) = f_1 x + f_2 y, \qquad (7)$$

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where $f_1 < f_2$, i.e., the fission rate is linear in the number of Cooperators and Defectors in the group, and more cooperative groups are less likely to fission. For the hybrid and PDE models, the fissioning density is the continuous uniform density[1];

$$f((x,y),(u,v)) = \begin{cases} \frac{2}{xy} & \text{if } (0,0) \leq (u,v) \leq (x,y) \\ 0 & \text{otherwise} \end{cases} \tag{8}$$

i.e., all possible outcomes of the fissioning of an (x,y)-group are equally likely. In the simulation model the fissioning density is a discrete uniform, i.e., $f((x,y),(u,v)) = 2/(x+1)(y+1)$. Finally, the extinction rate for an (x,y)-group is

$$E_\theta(x,y) = e_1 G(t) e^{-(e_2 x + e_3 y)}, \tag{9}$$

where $e_2 > e_3$, i.e, extinctions are more common in environments with more groups, less common in big groups than small groups, and less common in cooperative groups than non-cooperative groups. Since the groups cannot get arbitrarily large, the per-group fissioning rates are bounded. On the other hand, the per-group extinction rates are proportional to the number of groups in the environment. The population of groups in the environment therefore cannot grow indefinitely, and eventually reaches a stable size that depends (in a complicated way) on the equilibrium mixture of group-types.

There are many different kinds of evolutionary trajectories and equilibrium configurations possible within the constraints of the generic rate functions just described. In the following examples, the evolutionary trajectories that lead from the initial states to the equilibrium configurations are all quite different. In the first three examples the cost of cooperating, c, is varied while the other parameters are fixed. When c is small, cooperative groups dominate, but as c increases, the equilibrium environment contains fewer cooperative groups, until a point is reached where cooperation struggles to establish itself. In the fourth example, the parameters are set so that group level events are relatively rare, and cooperation relatively cheap. The result is an equilibrium where most groups are at or near an equilibrium size, but the internal composition of the groups vary.

The animation of the PDE solutions show the environment changing over time as a continuous density function that gradually morphs into an equilibrium configuration. We animate the view of the density function from above, with color coding representing the relative height. The animations of the hybrid and simulation solutions show the life histories of the groups, which appear as small "moving" circles. The circles generally move in a counter-clockwise direction, due to the fact that Defectors make gains in every group. The life histories of the groups in the simulation solutions are much more irregular than those in the hybrid solution due to the additional randomness. All the calculation for the following examples, and the assembly of the animations, were done with Matlab, and then uploaded to YouTube.

Example 1

In the first example, the parameters associated with the rate functions (5)-(9) have the values:

$\beta = .04, \ b = .05, \ c = .015, \ \gamma = .0008, \ \mu_c = \mu_d = .05, \ f_1 = .0008, \ f_2 = .0014, \ e_1 = .02, \ e_2 = .2, \ e_3 = .15.$

The initial condition has approximately 500 groups that are all (approximately) $(2,38)$-groups, i.e., groups of mostly Defectors. In this example, cooperators do very well. Starting from an environment dominated by Defectors, the first cooperative groups appear at around $t = 200$, and by $t = 400$ they are firmly established. Cooperative groups make steady gains at the expense of less cooperative groups, and by $t = 1000$, the equilibrium configuration, where most groups are large and cooperative, has started to take shape. Note that in equilibrium there are still a fair number of noncooperative groups, due to fissioning events and the

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[1]The factor of 2 in the uniform fissioning density (8) reflects the fact that the fissioning event results in two pieces, i.e., so that (2) is satisfied.

internal population dynamics of (formerly) cooperative groups. The dynamics that keep the equilibrium configuration stable are best seen in the hybrid solution. The overall evolutionary flow in this example is best seen in the PDE solution. The animations are on YouTube:

PDE Solution	http://www.youtube.com/watch?v=JwJY4RHjeHk&feature=plcp
Hybrid Solution	http://www.youtube.com/watch?v=jZolOyRm6s0&feature=plcp
Simulation Solution	http://www.youtube.com/watch?v=-n2kTnYJHC4&feature=plcp

Example 2

The parameter values in the second example are the same as in example 1, but the cost of cooperation, c, has been increased:

$$\beta = .04, \ b = .05, \ c = .020, \ \gamma = .0008, \ \mu_c = \mu_d = .05, \ f_1 = .0008, \ f_2 = .0014, \ e_1 = .02, \ e_2 = .2, \ e_3 = .15.$$

This time cooperative groups do not dominate. The equilibrium configuration is bimodal (best seen in the PDE solution), with a large number of cooperative groups and a large number of noncooperative groups, along with groups in various transitionary states. Like usual, the dynamics that keep the equilibrium configuration stable are best seen in the hybrid solution. The animations are on YouTube:

PDE Solution	http://www.youtube.com/watch?v=_mrCyJ9Fp0I&feature=relmfu
Hybrid Solution	http://www.youtube.com/watch?v=mxwo-JAeqxk&feature=relmfu
Simulation Solution	http://www.youtube.com/watch?v=2GeR_AkHBvs&feature=plcp

Example 3

In this example we increase the cost of cooperation to the point where large cooperative groups are rare in equilibrium.

$$\beta = .04, \ b = .05, \ c = .030, \ \gamma = .0008, \ \mu_c = \mu_d = .05, \ f_1 = .0008, \ f_2 = .0014, \ e_1 = .02, \ e_2 = .2, \ e_3 = .15.$$

To get an interesting animation, we start the process this time with about 200 very cooperative groups. At first the groups grow and multiply (due to fissioning events), but the cooperative groups gradually lose control of the environment. The overall evolutionary flow is best seen in the PDE solution, while the simulation and hybrid solutions show how a small number of cooperative groups manage to remain in equilibrium. The animations are on YouTube:

PDE Solution	http://www.youtube.com/watch?v=pTKQ6ghjJtk&feature=plcp
Hybrid Solution	http://www.youtube.com/watch?v=ZVL9gA07D0M&feature=plcp
Simulation Solution	http://www.youtube.com/watch?v=3E_ov2wjSvE&feature=plcp

Example 4

This example is different from the first three. The goal here is to illustrate what happens when fissioning events are rare enough so that groups have time to reach their equilibrium size. The parameters are set to:

$$\beta = .04, \ b = .05, \ c = .004, \ \gamma = .0008, \ \mu_c = \mu_d = .05, \ f_1 = .0001, \ f_2 = .0002, \ e_1 = .2, \ e_2 = .25, \ e_3 = .15.$$

With a small fissioning rate like this, cooperation has a harder time establishing itself than in the first three examples, so the cost of cooperation is lowered to compensate. (The cost is still significant for the large groups.) In equilibrium, most groups in the environment are in states along the "diagonal line" between (0,50) and (87.5,0). (It's actually not quite linear.) The occasional fissioning produces enough small cooperative groups to replace the large ones that become less cooperative over time. Note that both the PDE

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solution and the hybrid solution concentrate most of the groups right on the diagonal "line". This is due to the fact that those solutions are "large-population limits" of the simulation model, and when groups are large, it is very unlikely for them to get much larger than their equilibrium size. (There is a large "negative drift" if they do.) Thus, in this example, it is the simulation solution that provides the most accurate portrayal of the population dynamics. The animations are on YouTube:

PDE Solution	http://www.youtube.com/watch?v=qyL_akxWs3A&feature=plcp
Hybrid Solution	http://www.youtube.com/watch?v=HqRfCBQ3vIQ&feature=context-cha
Simulation Solution	http://www.youtube.com/watch?v=pqT6dJFb6OA&feature=plcp

4   Discussion

Perhaps the most common opinion on group selection is that it is theoretically possible, but much too weak in practice to be responsible for any of the notable outcomes its proponents attribute to it. This opinion is usually justified by a combination of intuitive arguments, e.g., Dawkins (1976), Pinker (2012), and mathematical models designed to formalize the intuitive arguments, e.g. Maynard Smith (1964), West, et.al. (2008). The intuitive arguments, when applied to groups of Cooperators and Defectors, suggest that any group containing Defectors will soon be taken over by them due to their increased fitness over Cooperators, and the fact that it is impossible to keep Defectors from invading groups of Cooperators due to mutation, migration, and other methods of gene flow between groups. Thus, the occasional cooperative group that somehow materializes is soon lost. The evolution of cooperation, it is argued, requires something other than group selection, such as kin recognition, limited dispersal, direct or indirect reciprocity, etc., e.g., West, et.al. (2008). The solutions of our models of two-level population dynamics suggest that the common wisdom on group selection is wrong. Group selection has a significant effect under a wide variety of conditions, and under the right circumstances can be a very potent evolutionary force. The key is to understand group selection as a dynamical process that occurs over evolutionary time scales, and not just as statistical properties of genetic changes from one generation to the next, Simon, et.al. (2012b).

We have explicitly shown that if there are enough fissioning events, enough variation between the offspring groups produced by fissioning events, and enough of a selective advantage for more-cooperative groups, then cooperation will thrive quite easily in the environment, without any additional assumptions (like kin recognition, limited dispersal, direct or indirect reciprocity, etc.). The physical process of group selection can be clearly seen in the animations of the simulation and hybrid dynamics as the "circulation" of group-types over time, where small cooperative groups formed by chance from fissioning events, grow and replace the existing large groups that have become less cooperative due to internal population dynamics.

A skeptic might argue that the parameter values we chose in our examples here (and elsewhere) that exhibited strong group selection must be wildly unrealistic, favoring Cooperators. In fact, the parameters chosen for the examples here are rather conservative in that respect. In examples 1 and 2, the cost of cooperation, c, is fairly large compared to the individual-level birth rates (i.e., $c \approx .02$ vs. $\beta + bx/(x + y) < .09$), and even larger compared to the net growth rates (birth rate minus death rate), especially for larger groups where the net growth rate is small. Even in example 1, where $c = .015$, Cooperators are at a significant disadvantage within the groups. Likewise, the mutation probability, $\mu_c = .05$, for Cooperators is large, making it impossible for cooperative groups to avoid being invaded by Defectors. On the other hand, the selective advantage for cooperative groups due to differences in the extinction rate function (i.e., $e_2 = .20$ vs. $e_3 = .15$) is not exceptional, and the difference in fissioning rates (i.e., $f_1 = .0008$ vs $f_2 = .0014$) actually produces more offspring for uncooperative groups.

Of course, group selection is not all-powerful. Example 3 shows that, as one would expect, if the cost of cooperation is too high then group selection is not strong enough to overcome it, and Defectors eventually dominate the environment. Similar results occur if there is insufficient fissioning, insufficient difference in

extinction rates between cooperative and uncooperative groups, or any of a number of other combinations of model features.

Finally, it is commonly believed that group selection is impossible unless the group-level reproductive rate (the fissioning rate) is larger than, or perhaps comparable to, the individual-level birth rates, e.g., Pinker (2012). If this belief were true, then group selection would be powerless except in very unlikely conditions; but as our animations show clearly, the belief is false. For instance, by following the trajectories of the groups in the simulation and hybrid animations in example 4, one can see that many groups (especially the small to mid-sized cooperative groups) survive long enough for numerous (10 to 20 or more) generations of their individuals to occur before they finally fission or die of extinction. Even in examples 1 and 2, where the fissioning rate is much larger, most groups survive for at least a few generations. In general, whether or not group selection is strong enough to allow cooperation to establish and maintain itself in the environment (or just to speed up the process) in a given example is impossible to guess. The dynamical equations need to be solved to be sure. We have shown that solutions of the dynamical equations can be numerically obtained in at least three different and informative ways, and the results can be animated, so models of two-level population processes can be studied in detail.

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