SUPPLEMENTARY INFORMATION

for Group-Level Events are "Catalysts" in the Evolution of Cooperation

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A1: Construction and Solution of the Model

The model predicts the dynamics of a population of groups made up of cooperators and defectors. Within groups, individuals play Prisoner's Dilemma with their group-mates, but the pairings are not completely random. A parameter $r \in [0,1]$ quantifies the nonrandomness. An individual chooses a partner of the same type (cooperator or defector) with probability r, and chooses a partner randomly from the whole group with probability $1-r$. We refer to this kind of "kin recognition" model as an r-process[10,13,14]. In an (x,y)-group (a group with x cooperators and y defectors) it follows that the probability a cooperator plays a cooperator and a defector plays a cooperator are (respectively)

$$P(C|C) = r + (1-r)\frac{x}{x+y}, \quad \text{and} \quad P(C|D) = (1-r)\frac{x}{x+y},$$

So $P(C|C) - P(C|D) = r$, which means that r is the relatedness within the groups as it is usually defined in the kin selection literature[17]. (Note that $P(D|D) - P(D|C) = r$ as well.)

The payoffs for the Prisioner's Dilemma game have the form

$$\begin{bmatrix} R & S \\ T & P \end{bmatrix} = \begin{bmatrix} 1 & 1 \\ 1 & 1 \end{bmatrix} + \begin{bmatrix} b-c & -c \\ b & 0 \end{bmatrix}$$

where b and c are the benefit and cost associated with the behavior of cooperators[1].

The expected payoffs for cooperators and defectors in an (x,y)-group are therefore

$$\beta_c(x,y) = r(1+b-c) + (1-r)\left(\frac{x}{x+y}(1+b-c) + \frac{y}{x+y}(1-c)\right),$$

[1] This is the usual "weak selection" setup, where we have set the "strength of selection" term to 1.

and

$$\beta_d(x,y) = r + (1-r)\left(\frac{x}{x+y}(1+b) + \frac{y}{x+y}\right).$$

Birth rates of cooperators and defectors in an (x,y)-group are $s\beta_c(x,y)$ and $s\beta_d(x,y)$, where $s > 0$ is the birth rate parameter. The death rates for both cooperators and defectors in an (x,y)-group is proportional to the size of the group, i.e. $d(x+y)$, where $d > 0$ is the death rate parameter. There is also migration in the model. Each individual migrates from its group at rate μ and joins another group at random. Let C and D be the total number of cooperators and defectors in the population (summed over all the groups), and let G be the number of groups. The total rate that cooperators migrate away from an (x,y)-group is μx, and the rate that cooperators migrate to a given group is $\mu\frac{C}{G}$. (Note: $\frac{C}{G}$ is the average number of cooperators per group.) Likewise defectors migrate away from an (x,y)-group at rate μy and migrate into it at rate $\mu\frac{D}{G}$.

Of course, the intra-group populations x and y are actually dynamical variables, $x(t)$ and $y(t)$, and likewise, the total populations, C_t, D_t, and G_t are also functions of time. In this article birth and death rates are interpreted as deterministic rates[2], which leads to a real-valued population process governed by the differential equations

$$\begin{bmatrix} x' \\ y' \end{bmatrix} = \begin{bmatrix} s\beta_c(x,y)x - d(x+y)x + \mu(\frac{C_t}{G_t} - x) \\ s\beta_d(x,y)y - d(x+y)y + \mu(\frac{D_t}{G_t} - y) \end{bmatrix} \equiv \begin{bmatrix} \alpha_t^c \\ \alpha_t^d \end{bmatrix}. \tag{1}$$

Two things can happen to a group as it ages. It can die of extinction, which means all the individuals in the group sudenly die; or it can fission, which means it breaks into pieces that become new autonomous groups. The state of the whole population at time t is given by a density function $\theta_t(x,y)$ where $\theta_t(x,y)dydx$ can be thought of as the number of (x,y)-groups in the population at time t. Equation (1) in the main text governs the dynamics for $\theta_t(x,y)$[8]. Virtually any quantity

[2] If we interpret the birth and death rates as stochastic rates then $x(t)$ and $y(t)$ are integer-valued, and the individual-level population process is a continuous-time Markov chain[8].

associated with the model can be calculated from $\theta_t(x,y)$; in particular,

$$G_t = \int\int \theta_t(x,y)dydx, \qquad C_t = \int\int x\theta_t(x,y)dydx, \qquad \text{and} \qquad D_t = \int\int y\theta_t(x,y)dydx. \quad (2)$$

In the model, an (x,y)-group fissions at rate

$$f(x,y) = \lambda(x+y), \quad (3)$$

where $\lambda \geq 0$ is the fission rate parameter.

The extinction rate in the model is

$$e(x,y,G) = \frac{e_0 G}{(\phi x + y)^2}, \quad (4)$$

where $e_0 \geq 0$ is the extinction rate parameter, and ϕ is the selective extinction parameter. Thus, smaller groups are more likely to die, and groups are more likely to die when there are more groups to compete with. If $\phi = 1$ then the extinction rate depends on the size of the group, but does not distinguish between cooperative and uncooperative groups. If $\phi > 1$ then cooperative groups are favored.

When a group fissions the outcome is specified (statistically) by a fissioning density[8]. A fissioning density is a function $h((x,y),(u,v))$ where $h((x,y),(u,v))dydx$ is interpreted as the expected number of (x,y)-groups resulting from the fissioning of a (u,v)-group. For (u,v) fixed, $h((x,y),(u,v))$ is a function with support on $[0,u] \times [0,v]$, whose integral over that region is equal to 2 (since a fission event results in two pieces), and whose mean is $(x/2, y/2)$. The fissioning density used in the model is a weighted average of a uniform density and a discrete density, yielding a simple example of associative splitting. The "uniform" density, where all possible outcomes of the fissioning of an (x,y)-group are equally likely, is $h_1((x,y),(u,v)) = \frac{2}{uv}$, and the discrete density is $h_2((x,y),(u,v)) = \delta_{((x,y)=(0,v/2))} + \delta_{((x,y)=(u,y/2))}$, where $\delta_{(\cdot)}$ is the delta function. In our model the fissioning density is

$$h((x,y),(u,v)) = (1-\psi)h_1((x,y),(u,v)) + \psi h_2((x,y),(u,v)), \tag{5}$$

where $\psi \in [0,1]$ is the associative splitting parameter. When $\psi = 0$ there is no associative splitting, so the outcomes of fission events are random (uniform). When $\psi = 1$, all the cooperators end up in the same piece.

Finally, the initial condition for dynamical equation is based on a bivariate Normal density,

$$\theta_0(x,y) = \frac{N_0}{2\pi v_0} e^{((x-C_0)^2+(y-D_0)^2)/2v_0}, \ \ (x,y) \geq 0.$$

The density is truncated off the positive quadrant, so $G_0 = \int\int \theta_0(x,y)dydx$ will be less than N_0, especially if (C_0, D_0) is close to one of the axes.

Solving the model means solving equation (1) from the main text using α_t^c and α_t^d from (1), and

$$g_t(x,y) = f(x,y) - e(x,y,G_t) + \int_x^\infty \int_y^\infty \theta_t(u,v)h((x,y),(u,v))dvdu,$$

where the first two terms on the right side are the fission and extinction rates from (3) and (4), and the third term is the rate that new (x,y)-groups are born due to larger groups fissioning. Even in the simplest examples there is no colsed-form solution for the PDE (1) in the main text, but the equation can be solved numerically without much difficulty (as long as one is patient). A single run yields θ_t, $t \in [0,T]$, which can take from a few finutes to a few hours, depending on how big T is. The Matlab program we used for our numerical experiments is linked to in the Methods section.

A2: The Benchmark Model, and some "Back of the Envelope" Calculations

Table 1 lists the benchmark (default) values in our experiments, although the figures in the main text allow r, ρ, μ, ϕ, and ψ to vary. Note that in the benchmark settings, $rb < c$, so Hamilton's rule predicts (correctly) that cooperation cannot thrive by pure kin selection ($\rho = 0$). However, $\rho = 1.0$ in the benchmark model, and cooperation establishes itself quite easily in that case. Note also that

Table 1: **Model Parameters and their Benchmark Values**

Parameter	Description	Benchmark Value
r	intra-group relatedness	0.2
ρ	group-level event rate scaling factor	1.0
b	benefit associated with cooperation	0.4
c	cost associated with cooperation	0.1
d	individual death rate parameter	0.0005
s	game payoff to birth rate scaling factor	0.025
e_0	extinction rate scaling factor	0.025
ϕ	selective extinction parameter	1.0
λ	fission rate scaling factor	0.00025
ψ	associative splitting parameter	0.0
μ	per individual migration rate	0.0025
N_0	initial number of groups	471.25
(C_0, D_0)	initial mean group type	(2,48)
v_0	initial group type variance	5.0

G_0, the initial number of groups is 384.75 in all our examples and not $N_0 = 471.25$. The reason for this is that since the initial group mean is so close to the y axis, a sizable fraction of the initial density is truncated.

The only way to determine the precise model dynamics and equilibrium configuration based on the model parameter setings is to solve equation (1) from the main text. However, there are some simple heuristic calculations that give good estimates of some of the important quantities associated with the model, like stable group sizes, average group lifetimes, and group birth and death rates. These kinds of calculations allowed us to quickly calibrate the parameters to be in line with hunter gatherer dynamics. The following analysis consists of "back of the envelope" calculations, which can be useful for quick approximations.

Starting with the population dynamics within the groups, we can determine the approximate quilibrium group sizes from b, c, d, and s. In a group of mostly cooperators ($y \approx 0$), the per-individual birth rate is $s\beta_c(x,y) \approx s(1+b-c)$ which equals 0.0325 in our benchmark model. The total birth rate in the group is therefore about $0.0325\tau_c$, where τ_c is the equilibrium size of a group of cooperators. The per-individual death rate is $d\tau_c$, so in our benchmark model the total death rate in a group of cooperators is $0.0005\tau_c^2$. Since the total birth rate and total death rate are equal in equilibrium, we obtain $\tau_c = 65$. Likewise, a group of (mostly) defectors has a total birth rate of about $0.025\tau_d$ and a total death rate of $0.0005\tau_d^2$, so we obtain $\tau_d = 50$. Groups with a mixture of cooperators and defectors will have an equilibrium size somewhere between 50 and 65. This is why the diagonal line between $(0,50)$ and $(65,0)$ appears to be a boundary in Figure 2 in the main text. For simplicity (precision is neither necessary nor possible in these kinds of calculations), we will use $\tau = 60$ as the size of a typical mature group in our numerical experiments. Thus, the per-individual death rate in a typical group is $\tau d = 0.03$, meaning that the average lifetime is about $1/\tau d \approx 33$ time units. If we accept that hunter gatherers lived a bit more that 30 years on the average then it follows that one time unit in the model corresponds to about 1 year.

Now that we know the time unit we can estimate how often other events occur. The benchmark migration rate is $\mu = .0025$, which means that the probability an individual migrates away from the tribe in one year is about 1/400. In a group of 60 this means somebody is migrating away about once every 6.7 years. (And every group can expect a migrant to join them about once every 6.7.)

A group of size 60 will fission at rate $60\lambda = .015$ per time unit; in other words it will take a group about 66 years on the average to fission after it reaches full size (if the group doesn't die of extinction first). Recall that smaller groups are less likely to fission in the model.

To estimate the average time a group lives before extinction (if it doesn't fission first) we need the equilibrium number of groups in the population. This quantity is difficult to estimate directly from the basic model parameters since the sizes of the groups in the population vary so much. However, we see from the numerical experiments that the equilibrium number of groups was typically around 400, which will suffice for our estimates here. If we use $G = 400$ then the extinction rate of a group of 60 is about $e_0 \cdot 400/60^2 = 1/360$, which means a mature group can expect to live about 360 years if it doesn't fission first. However, a group of only 30 individuals has an extinction rate 4 times as large, and smaller groups are even more vulnerable. New groups (fissioned pieces) often start out small and therefore face the threat of extinction until they grow bigger.

The lifetime of a group is the time from when it is born until it either fissions or dies of extinction. We see that a mature group will fission after about 66 years on the average, if it doesn't go extinct first; and a mature group will die of extinction after about 360 years on the average, if it doesn't fission first. Another quantity of interest is the time it takes a fissioned piece to reach maturity. We can approximate the time using a logistic equation (since the growth is approximately logistic)

$$P(t) = \frac{p_e}{1 + \frac{p_e - p_0}{p_0} e^{-st}},$$

where p_e is the equilibrium population, p_0 is the initial population, and $s = .025$ is the birth rate scaling parameter. If we use $p_e = 60$, as we do above, then a group of size $p_0 = 25$ needs about 64 years to reach size 50. Thus, the average time from when a new group is born from a fission event until it fissions (assuming it does not die of extinction first, and does not fission until it reaches maturity) is (roughly) the time a group of 25 takes to grow to size 50, plus the time a mature group takes to fission, which is $64 + 66 = 130$ years.

A3: Intra-Group vs. Population-Wide Relatedness

The population dynamics within groups is an r-process, so the relatedness within every group, at all times, is r. However, the situation is not nearly as simple if one considers the population as a whole. The population-wide relatedness (as it is usually defined in the literature) can be computed from $\theta_t(x,y)$, but it is a rather complicated and unintuitive quantity. The population-wide relatedness is not used in any way in this article, but for completeness and to satisfy curious readers it is derived next.

Let $\hat{\theta}_t(x,y) = \theta_t(x,y)/G_t$, where G_t is the number of groups at time t given by (2). Thus, $\hat{\theta}_t(x,y)$ is a proper probability density which can be interpreted as the probability a randomly chosen group is an (x,y)-group. Let $\hat{\theta}^c_t(x,y) = x\hat{\theta}_t(x,y)/C_t$ and $\theta^d_t(x,y) = y\theta_t(x,y)/D_t$ be the states of the population as seen by a random cooperator and defector, respectively, where C_t and D_t are given by (2). The probability a random cooperator is paired with another cooperator at time t is therefore $\int\int \theta^c_t(x,y)(r + (1-r)\frac{x}{x+y})dydx$ and the probability a random defector is paired with a cooperator at time t is $\int\int \theta_t^d(x,y)(1-r)\frac{x}{x+y}dydx$. Thus, at time t,

$$P(C|C) = r + (1-r)E_t\left(\frac{X^2}{X+Y}\right)/C_t$$

$$P(C|D) = (1-r)E_t\left(\frac{XY}{X+Y}\right)/D_t,$$

where E_t is expectation with respect to the density $\hat{\theta}_t$, and X and Y are the (random) numbers of cooperators and defectors in a group chosen randomly from the population at time t. Since $C_t = E_t(X)$ and $D_t = E_t(Y)$, the population-wide relatedness at time t is

$$R_t = P(C|C) - P(C|D) = r + (1-r)\left(E_t\left(\frac{X^2}{X+Y}\right)E_t(X)^{-1} - E_t\left(\frac{XY}{X+Y}\right)E_t(Y)^{-1}\right)$$

which is time dependent, and has no obvious causal connection with the overall population dynamics.