



Hamilton's rule in multi-level selection models

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ABSTRACT

Hamilton's rule is regarded as a useful tool in the understanding of social evolution, but it relies on restrictive, overly simple assumptions. Here we model more realistic situations, in which the traditional Hamilton's rule generally fails to predict the direction of selection. We offer modifications that allow accurate predictions, but also show that these Hamilton's rule type inequalities do not predict long-term outcomes. To illustrate these issues we propose a two-level selection model for the evolution of cooperation. The model describes the dynamics of a population of groups of cooperators and defectors of various sizes and compositions and contains birth–death processes at both the individual level and the group level. We derive Hamilton-like inequalities that accurately predict short-term evolutionary change, but do not reliably predict long-term evolutionary dynamics. Over evolutionary time, cooperators and defectors can repeatedly change roles as the favored type, because the amount of assortment between cooperators changes in complicated ways due to both individual-level and group-level processes. The equation that governs the dynamics of cooperator/defector assortment is a certain partial differential equation, which can be solved numerically, but whose behaviour cannot be predicted by Hamilton's rules, because Hamilton's rules only contain first-derivative information. In addition, Hamilton's rules are sensitive to demographic fitness effects such as local crowding, and hence models that assume constant group sizes are not equivalent to models like ours that relax that assumption. In the long-run, the group distribution typically reaches an equilibrium, in which case Hamilton's rules necessarily become equalities.

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1. Introduction

Models for the evolution of cooperation are often formulated in terms of public goods interactions: individuals either produce a benefit b at a cost c , so that the benefit accrues to all individuals in an interaction group, or they make no contribution at no cost. The question is, under what conditions are genes coding for making a contribution b to the public good maintained in the population? One general answer is that interactions need to be assortative, so that individuals carrying genes coding for cooperation interact, on average, more often with cooperating individuals than individuals carrying genes coding for defection (Fletcher and Doebeli, 2009). Therefore, to understand the evolution of cooperation we need to understand the biological mechanisms that generate such assortment.

Inclusive fitness theory (Hamilton, 1964; van Veelen, 2007) has long been used as one particular method of taking stock of the

degree of assortment. In this framework, the condition for cooperation to be selectively favoured is often given in the form:

$$rb > c, \quad (1)$$

where r is in general some measure of the population structure (Queller, 1985). In particular, r is often taken to be the average relatedness of interacting individuals, as compared to the average relatedness in the population, in which case inequality (1) is referred to as Hamilton's rule. It is important to note that inequality (1) is only a description of whether the current level of assortment as subsumed in the parameter r is sufficient to favour cooperation, but not a description of the mechanisms that would lead to such assortment. It has been suggested repeatedly that the problem of cooperation can be understood entirely based on Hamilton's rules of the form (1). Even though often taken as gospel, this claim is wrong in general, for two reasons.

First, and foremost, even if a rule of the form (1) predicts the direction of selection for cooperation at a given point in time, the long-term evolution of cooperation cannot be understood without having a dynamic equation for the quantity r , i.e., without understanding the temporal dynamics of assortment. The dynamics of r in

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turn cannot be understood based solely on the current level of cooperation, and hence expressions of type (1) are in general insufficient to describe the evolutionary dynamics of cooperation. Second, the quantity r , which measures the average relatedness among interacting individuals, is insufficient to construct Hamilton's rule in models that account for variable individual-level death rates and/or group-level events.

In this article we present a model for the evolution of cooperation in which the validity of these claims is apparent. The model is based on the well-known public goods game, which is played in groups of various sizes. The model is deterministic, and an isolated interaction group is characterized by the density x of cooperators and the density y of defectors, so that the total density of individuals in an (x,y) -group is $x+y$. The distribution of groups of different compositions is given by a density distribution $\theta_t(x,y)$, which generally varies over time t . (Thus, $\theta_t(x,y) dy dx$ is approximately the density of groups with the density of cooperators in the interval $(x,x+dx)$ and the density of defectors in the interval $(y,y+dy)$.) In each interaction group, individuals are playing a public goods game, so that each cooperator is contributing a benefit b to the public good at a cost c , and each defector is contributing nothing at no cost. As a consequence, the payoff to a cooperator in an (x,y) -group is $bx/(x+y)-c$, and the payoff to a defector in an (x,y) -group is $bx/(x+y)$. These payoffs are used to define per capita birth rates in each group, which along with the group-size dependent death rates determine the ecological dynamics in each group. In particular, the public goods interactions are not only involved in the frequency dynamics of cooperators and defectors in each group, but also the dynamics of the total density $x+y$ of each group. This generates part of the dynamics of the distribution $\theta_t(x,y)$.

In addition, the dynamics of $\theta_t(x,y)$ can be influenced by group-level events. Specifically, we assume that groups can go extinct, and that groups can fission and thereby give rise to offspring groups whose composition is related to the composition of the parent group. Fissioning and extinction rates are in general functions of group composition, but also of the total density of groups in the whole evolving population. Because the model incorporates birth and death events at both the individual and the group level, the model is a full multi-level selection model for the evolution of cooperation (Okasha, 2006). We will show that in this model, rules of type (1) are of very limited use, because they do not predict long-term evolutionary dynamics, and because even though the instantaneous dynamics is always reflected in such a rule, the rule is in general very complicated and does not have a straightforward biological interpretation, e.g. in terms of relatedness.

2. A two-level selection model

Consider a population that is made of distinct groups of individuals. There are two types of individuals: cooperators and defectors. For $x \geq 0$, $y \geq 0$, define an (x,y) -group to be a group in which the density of cooperators is x and the density of defectors is y . x and y , as well as time t , are continuous variables, hence the population dynamics is governed by differential equations. Discrete-stochastic versions of the present model can also be studied, and in many cases the results are qualitatively very similar; see Simon (2008, 2010), Puhalskii and Simon (2011).

The state of the population at time t is specified by an accounting of how many (x,y) -groups are present at time t , i.e., a density function $\theta_t(x,y)$. Virtually any quantity associated with the population at time t can be calculated from $\theta_t(x,y)$. In particular,

$$G(t) = \int \int \theta_t(x,y) dy dx \quad (2)$$

is the total density of groups in the population, and

$$C(t) = \int \int x \theta_t(x,y) dy dx, \quad \text{and} \quad D(t) = \int \int y \theta_t(x,y) dy dx \quad (3)$$

are the total densities of cooperators and defectors in the population. Throughout this paper, double integrals denote an integral over the nonnegative quadrant, and the variable t will be omitted in formulas that do not explicitly involve time.

Within a given group, let $(x(t), y(t))$ be the densities of cooperators and defectors at time t . The population dynamics is governed by the pair of differential equations:

$$\begin{bmatrix} x' \\ y' \end{bmatrix} = \begin{bmatrix} \alpha_c(x,y) \\ \alpha_d(x,y) \end{bmatrix},$$

where

$$\alpha_c(x,y) = (B_c(x,y) - D_c(x,y))x \quad \text{and} \quad \alpha_d(x,y) = (B_d(x,y) - D_d(x,y))y. \quad (4)$$

$B_c(x,y)$ and $B_d(x,y)$ are the per capita birth rates of cooperators and defectors in an (x,y) -group, and $D_c(x,y)$ and $D_d(x,y)$ are the per capita death rates of cooperators and defectors in an (x,y) -group. Based on the assumption of public goods interactions taking place in each group, we assume that these rates are given as

$$B_c(x,y) = \beta + \frac{x}{x+y}b - c, \quad B_d(x,y) = \beta + \frac{x}{x+y}b, \quad (5)$$

and

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

The reasoning behind these choices is as follows. An individual's birth rate has a nominal value of β . Its birth rate is increased by a benefit provided by the cooperators in its group, but the benefit is shared by the whole group. Thus, in an (x,y) -group the x cooperators provide a total benefit of xb , so each individual in the group gets $xb/(x+y)$. Cooperators pay a cost, c , for providing the benefit. The death rate is proportional to the population of the group, and is the same for cooperators and defectors. Note that in our model of individual-level population dynamics, the total population $x+y$ is free to vary in time, unlike many standard models such as the replicator equation (Nowak, 2006), which constrain the total population to a constant value. The density-dependent birth and death rates we use in (5) and (6) ensure that group sizes reach an equilibrium.

A slight modification to (4) allows us to include mutation in our model. Suppose cooperators give birth to defectors with probability $\mu_c \geq 0$ and defectors give birth to cooperators with probability $\mu_d \geq 0$. Then the rates of change of cooperators and defectors in an (x,y) -group are

$$\alpha_c(x,y) = \left(\beta + \frac{x}{x+y}b - c \right) (1 - \mu_c)x + \left(\beta + \frac{x}{x+y}b \right) \mu_d y - (x+y)\gamma \quad (7)$$

and

$$\alpha_d(x,y) = \left(\beta + \frac{x}{x+y}b \right) (1 - \mu_d)y + \left(\beta + \frac{x}{x+y}b - c \right) \mu_c x - (x+y)\gamma. \quad (8)$$

If $\mu_c = \mu_d = 0$ then (7) and (8) reduce to (4).

Due to the assumption of public goods interactions, in the absence of mutation the fate of every group in isolation is the same: cooperation goes extinct, and the defectors reach an equilibrium population density given by β/γ . If $\mu_d > 0$ then there will always be a (small) positive fraction of cooperators sustained by mutation.

A crucial property of our individual-level birth-death dynamics is that group-size varies in time, and tends towards an equilibrium level. In particular, a small group (e.g. a fissioned piece) can grow into a large one, especially if it contains a sizable fraction of cooperators. But as time goes on, the fraction of

cooperators in each group decreases, with the rate of decrease depending on c , the cost of cooperation.

At the group level there are two kinds of events in our model: fissioning and extinction (see Simon, 2010 for an example incorporating additional group-level events in the form of games between groups). Extinction of a group is the simultaneous death of all its members. In our model, extinction is governed by a rate function $e_t(x,y)$ which depends on the composition of the group, and also on the state of the whole population. One can think of $e_t(x,y)\Delta$ as the probability that an (x,y) -group will go extinct in the next Δ time units. In this paper, the extinction rate will have the form

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

where e_1, e_2, e_3 are nonnegative constants. The rationale for this choice is that group extinction is more common when the density of groups is high, and it is less likely for larger groups. If $e_2 > e_3$ then more cooperative groups are less prone to extinction.

When a group fissions, it breaks apart into two or more pieces, each of which becomes a new group. Thus, extinction is how groups die and fissioning is how groups are born. (Technically, after a group fissions it no longer exists as a group, but some or all of the individuals in the original group survive in the fissioned pieces.) Just as the sizes and compositions of the groups change in time due to individual-level births and deaths, the density of groups in the population changes in time due to group-level births and deaths.

The fissioning process is governed by a fissioning rate function, $f(x,y)$, and a fissioning density $h[(u,v),(x,y)]$. One can think of $f(x,y)\Delta$ as the probability that an (x,y) -group will fission in the next Δ time units. In this paper, the fissioning rate will have the form:

$$f(x,y) = f_1 x + f_2 y, \tag{10}$$

where f_1 and f_2 are nonnegative constants. The rationale for this choice is that larger groups are more likely to fission than smaller groups, and (if $f_1 \neq f_2$) the fissioning rate depends on the composition of the group. In our model, the fissioning rate of an (x,y) -group only depends on x and y , so no subscript t is needed. The fissioning density, $h[(u,v),(x,y)], (0,0) < (u,v) < (x,y)$, quantifies the result of the fissioning of an (x,y) -group.

In general, one can interpret $h[(u,v),(x,y)] dv du$ as the expected number of (approximately) (u,v) -groups resulting from the fissioning of an (x,y) -group. A fissioning density will always satisfy $\int_0^x \int_0^y u h[(u,v),(x,y)] dv du \leq x$ and $\int_0^x \int_0^y v h[(u,v),(x,y)] dv du \leq y$, since the total number of cooperators and defectors in the fissioned pieces cannot exceed the numbers in the original group.

In the examples in this paper we will use

$$h[(u,v),(x,y)] = \begin{cases} \frac{4e^{-2(u-x/2)^2/x} e^{-2(v-y/2)^2/y}}{\pi\sqrt{xy}} & (0,0) < (u,v) < (x,y) \\ 0 & \text{otherwise.} \end{cases} \tag{11}$$

Eq. (11) can be understood as a continuous (Normal) approximation of a certain binomial density. Suppose x and y are integers, and suppose that each individual in the original group flips a fair coin to determine which of two fissioned pieces to join. In that case the number of cooperators in each piece has mean $x/2$ and variance $x/4$; and likewise the number of defectors in each piece has mean $y/2$ and variance $y/4$. Eq. (11) is the bivariate Normal density that matches these means and variances, multiplied by 2 since there are two pieces. The advantage of the Normal approximation is that there is no requirement that x and y are integers, so (11) can be used in our continuous model.

Some of the probability mass in (11) is lost beyond the boundary. This can be remedied by multiplying the density by an appropriate factor, or the loss can be interpreted as individuals

that do not survive the fissioning process. We will choose the latter approach. There are many possible choices for fissioning densities, corresponding to different kinds of realignment. In fact, (11) is a special case of a two-parameter class of fissioning densities described in Simon (2010). We choose (11) here because it is the simplest member of that class and because it illustrates our main points very well.

The dynamical equation for our model is derived in generality in Simon (2010) (in that paper, migration of individuals between groups is also included in the model). It takes the form of a partial differential equation, which in our present model takes the form:

$$\frac{\partial \theta_t}{\partial t}(x,y) = \rho_t(x,y) - (e_t(x,y) + f(x,y))\theta_t(x,y) - \frac{\partial[\theta_t \alpha_c]}{\partial x}(x,y) - \frac{\partial[\theta_t \alpha_d]}{\partial y}(x,y), \tag{12}$$

where

$$\rho_t(x,y) = \int_x^\infty \int_y^\infty h[(x,y),(u,v)] f(u,v) \theta_t(u,v) dv du$$

is the rate that new (x,y) -groups are born due to larger groups fissioning at time t , $\alpha_c(x,y)$ and $\alpha_d(x,y)$ are given by (7) and (8), and $e_t(x,y)$ and $f(x,y)$ are given by (9) and (10). In the special case where there are no group-level events, Eq. (12) reduces to the conservation law:

$$\frac{\partial \theta_t}{\partial t}(x,y) + \frac{\partial[\theta_t \alpha_c]}{\partial x}(x,y) + \frac{\partial[\theta_t \alpha_d]}{\partial y}(x,y) = 0. \tag{13}$$

(Note that if there are no group-level events, then the total density of groups (2) is conserved.) Eqs. (12) and (13) are examples of hyperbolic partial differential equations, which arise in a variety of physical problems, and are well understood mathematically (Leveque, 1992). Eqs. (12) and (13) can be solved numerically, providing a complete dynamical analysis of our model. See Simon (2010) for a description of the numerical procedure used to solve the PDE and generate the figures, both in that paper and the present work.

3. Hamilton-like inequalities

In this section we show that Hamilton-like inequalities can be derived for our model, but they are in general quite different from the usual $rb > c$ form, where r is a measure of “relatedness” between individuals in the population. We begin by deriving Hamilton’s inequality for a model without group-level birth-death processes. The resulting model is very similar to the one studied in Fletcher and Doebeli (2009), but incorporates varying group sizes and variable death rates. We then analyze the differences caused by these changes. Let $\theta(x,y)$ be the distribution of groups that specifies the state of the population, and define

$$\hat{\theta}(x,y) = G^{-1} \theta(x,y),$$

where $G = \int \int \theta(x,y) dy dx$ is the density of groups in the environment. $\hat{\theta}(x,y)$ is a proper probability density function, i.e., $\hat{\theta}(x,y) dy dx$ can be interpreted as the probability a randomly chosen group is approximately an (x,y) -group. All expectations in this section are with respect to $\hat{\theta}(x,y)$. Our goal is to find conditions for cooperation to be favoured in such a population, i.e., for the total fraction of cooperators to be increasing at a given point in time. This happens if the average cooperator has a higher per capita growth rate than the average defector. Let X and Y be the numbers of cooperators and defectors in a randomly chosen group, i.e., $\hat{\theta}(x,y)$ is the joint density function for (X,Y) . From (3) it follows that

$$E(X) = C/G \quad \text{and} \quad E(Y) = D/G,$$

where C , D , and G are the total number of cooperators, defectors, and groups in the environment, respectively. If a cooperator is chosen at random from the environment, the probability it resides in an (x,y) -group is specified by the density function:

$$\hat{\theta}^c(x,y) = E(X)^{-1}x\hat{\theta}(x,y), \tag{14}$$

and the probability a randomly chosen defector resides in an (x,y) -group is specified by

$$\hat{\theta}^d(x,y) = E(Y)^{-1}y\hat{\theta}(x,y). \tag{15}$$

We will call (14) and (15) the cooperator-biased and defector-biased densities, respectively. Thus, if $Z(x,y)$ is a function of the state of a group, then the average value of $Z(x,y)$ as seen by a randomly chosen cooperator is

$$\int \int Z(x,y)\hat{\theta}^c(x,y) dy dx = E(X)^{-1}E(XZ(X,Y)),$$

and a randomly chosen defector sees

$$\int \int Z(x,y)\hat{\theta}^d(x,y) dy dx = E(Y)^{-1}E(YZ(X,Y)).$$

It follows that if $F_c(x,y)$ is the fitness of a cooperator in an (x,y) -group, and $F_d(x,y)$ is the fitness of a defector in an (x,y) -group, then in the environment as a whole, the average fitness of a cooperator is larger than the average fitness of a defector if

$$E(X)^{-1}E(XF_c(X,Y)) > E(Y)^{-1}E(YF_d(X,Y)). \tag{16}$$

To derive Hamilton's rule, it remains to choose the fitness functions, $F_c(x,y)$ and $F_d(x,y)$.

In populations in which individuals play a public goods game within their groups, the traditional definition of cooperator and defector fitness is their payoff from the game (e.g. Fletcher and Doebeli, 2009). In the present model this is

$$F_c(x,y) = \beta + \frac{x}{x+y}b - c \quad \text{and} \quad F_d(x,y) = \beta + \frac{x}{x+y}b.$$

From (16) it follows that cooperation is favored if

$$rb > c, \tag{17}$$

where

$$r = E(X)^{-1}E\left(\frac{X^2}{X+Y}\right) - E(Y)^{-1}E\left(\frac{XY}{X+Y}\right) \tag{18}$$

is a measure for assortment between cooperators. In fact, it can be shown that (18) is the same as Hamilton's covariance version of r (Hamilton, 1975), applied to the present setting (see Appendix).

The expression for r in (18) does not simplify in general. However, in the special case where all the groups have the same size N (and therefore the same death rates), there is some significant simplification. If $X+Y=N$ with probability one, then (18) reduces to

$$r = \frac{1}{N} \left(\frac{E(X^2)}{E(X)} - \frac{E(XY)}{E(Y)} \right) = \frac{\text{Var}(X)}{E(X)(N-E(X))}. \tag{19}$$

Note that

$$E(X)(N-E(X)) = E(NX) - E(X)^2 \geq E(X^2) - E(X)^2 = \text{Var}(X),$$

so $0 \leq r \leq 1$. Eq. (19) is equivalent to expression (2.3) in Fletcher and Doebeli (2009).

In the present model, (17) does not predict whether cooperation increases overall because it does not take the individual death rates into account. This is illustrated in Fig. 1(c), where the curve $r_t b$ is greater than c for all $t > 0$, implying (incorrectly) that cooperation should prevail. The death rates are density-dependent and therefore introduce non-additive fitness effects which cause Hamilton's rule (17) to fail (Queller, 1985; van Veelen, 2009, 2011). The following

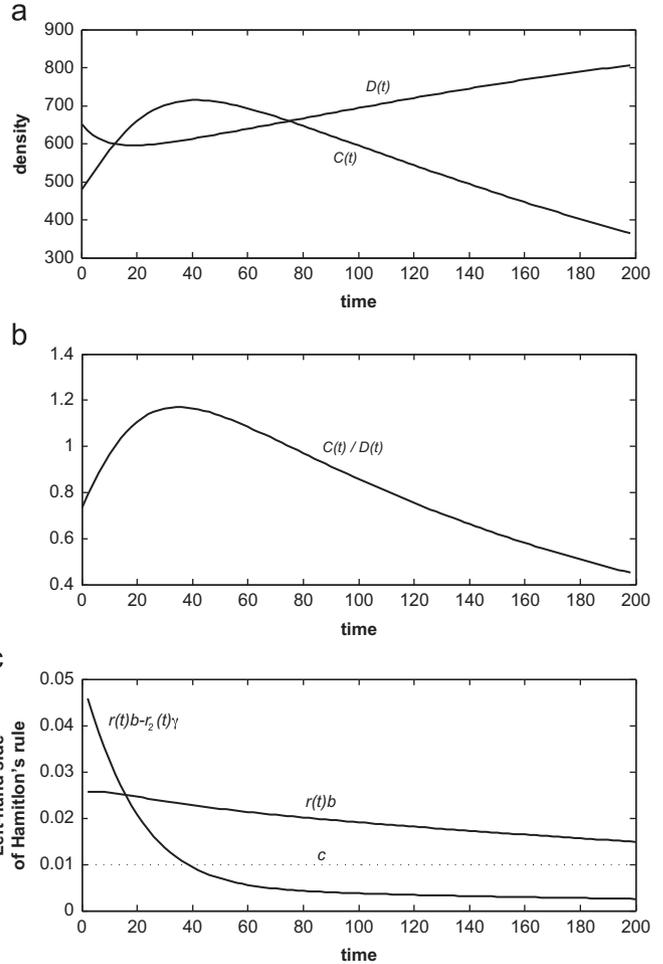


Fig. 1. Population dynamics for an example with no group-level events. The population dynamics are governed by (13). (a) shows the total density of cooperators $C(t)$ and defectors $D(t)$ in the population, and (b) shows the ratio $C(t)/D(t)$. In this example, the initial assortment is highly favourable to cooperators, so the ratio of cooperators to defectors increases at first, and cooperators gain a majority status at about $t=14.0$. However, the higher birth rate of defectors in each group makes it impossible for cooperators to maintain their advantage. At about $t=75.4$ the defectors regain their majority, and the cooperators eventually go extinct. (c) shows $r(t)b$, where $r(t)$ is derived from $\theta_t(x,y)$ via Eq. (18). Note that $r(t)b > c$ for all $t > 0$ so this form of Hamilton's rule predicts the wrong direction of selection for all $t > 36$. The other curve shows $r(t)b - r_2(t)\gamma$ which is derived from (20). This version of Hamilton's rule, which takes both births and deaths into account, correctly predicts whether cooperation is favored at each point in time. However, from (c) it is apparent that for all t using Hamilton's rule (17), and for $t < 36.0$ using Hamilton's rule (20), that these inequalities are "unaware" that cooperation is eventually doomed to extinction. For the numerical simulation, the initial density distribution was $\theta_0(x,y) = 1.5 \exp(-((x-10)^2 + (y-2)^2)/10) + \exp(-((x-2)^2 + (y-20)^2)/10), x,y > 0$. Integrating $\theta_0(x,y)$ yields the total density of groups at time 0, which is $G(0)=68.35$, and since there are no group-level events, this number does not change, i.e., $G(t)=G(0)$. The parameters for the individual-level birth-death dynamics (4) in this example are set to $b=0.05$, $c=0.01$, $\beta=0.04$, $\gamma=0.002$ (no mutation: $\mu_c = \mu_d = 0$). There are no group-level events, so $e_1 = f_1 = 0$.

version of Hamilton's rule takes both individual births and deaths into account.

This time we define an individual's fitness as its birth rate minus its death rate, i.e.,

$$F_c(x,y) = \alpha_c(x,y) \quad \text{and} \quad F_d(x,y) = \alpha_d(x,y).$$

where $\alpha_c(x,y)$ and $\alpha_d(x,y)$ are given by (4). Defined this way, fitness refers to the net short-term productivity of an individual. In this case, cooperators are favored if

$$rb - r_2\gamma > c, \tag{20}$$

where r given by (18), and

$$r_2 = E(X)^{-1}E(X(X+Y)) - E(Y)^{-1}E(Y(X+Y)).$$

This expression can be viewed as a modified Hamilton’s rule that takes kin competition into account, because it incorporates density-dependent death rates (see, e.g. Van Dyken, 2010 for more in-depth discussions of Hamilton’s rule in the presence of kin competition). Also, note that in the special case where $X+Y=N$ with probability one the death rates are the same for all individuals, so we get $r_2=0$, and Hamilton’s rule is the same as before. However, in general there can be significant differences.

When mutation is included in the model it is no longer possible to determine whether or not cooperation is favored by using (16). Instead, we have to take a closer look at what it really means for cooperation to be favored at a particular point in time. In general, cooperation is favored in a population if the fraction of cooperators in the population is increasing. This is equivalent to the condition:

$$\frac{C'(t)}{C(t)} > \frac{D'(t)}{D(t)}. \tag{21}$$

We will take (21) as our definition for cooperators being favored at time t , since it is consistent with (16), (17), and (20) when they are applicable.

When mutation is included in our model, the total rate that cooperation increases in an (x,y) -group is $B_c(x,y)(1-\mu_c)x + B_d(x,y)\mu_d y - D_c(x,y)x$, and the rate that defectors increase is $B_d(x,y)(1-\mu_d)y + B_c(x,y)\mu_c x - D_d(x,y)y$. By integrating those terms against $\theta(x,y)$ we get the total rates cooperators and defectors increase in the population. Dividing by their total populations and simplifying yields a Hamilton-like rule for cooperation to be favored:

$$\tilde{r}b + r_2\gamma + r_3\beta > c \left(1 - \mu_c \left(1 + \frac{E(X)}{E(Y)}\right)\right), \tag{22}$$

where

$$\tilde{r} = E\left(\frac{X^2}{X+Y}\right) \left(\frac{1-\mu_c}{E(X)} - \frac{\mu_c}{E(Y)}\right) - E\left(\frac{XY}{X+Y}\right) \left(\frac{1-\mu_d}{E(Y)} - \frac{\mu_d}{E(X)}\right),$$

$$r_3 = \mu_d \left(1 + \frac{E(Y)}{E(X)}\right) - \mu_c \left(1 + \frac{E(X)}{E(Y)}\right),$$

and r_2 is the same as in (20). If $\mu_c = \mu_d = 0$ then $\tilde{r} = r$, $r_3 = 0$, and (22) reduces to (20).

The Hamilton-like rule (22) contains enough information to correctly predict the instantaneous direction and magnitude of evolutionary change in our dynamical model, as long as there are no group-level events. In particular, it correctly predicts whether or not cooperation is favored at any given point in time. This is illustrated in Fig. 1(b) and (c), where one can see that the ratio of cooperators to defectors changes from increasing to decreasing exactly when (22) is an equality. However, it is important to note that (22) does not necessarily predict the long-term evolutionary behaviour, because (as in Fig. 1) it may happen that at some point in time the group composition is such that cooperation is temporarily increasing, so that (22) is satisfied, despite the fact that (without group-level events) cooperation is doomed in the long-run. It is apparent from (21) that Hamilton’s rule contains no more than first-derivative information, so it cannot predict or explain the kinds of long-term dynamics that occur in the example of Fig. 1.

The Hamilton-like inequalities (17), (20) and (22) were derived from our model in the absence of group-level events. In that case, per capita birth and death rates (as well as mutation rates) determine the evolutionary dynamics, so Hamilton-type rules will accurately predict short-term evolutionary change. (No more than this, though, as such rules do generally not predict long-term

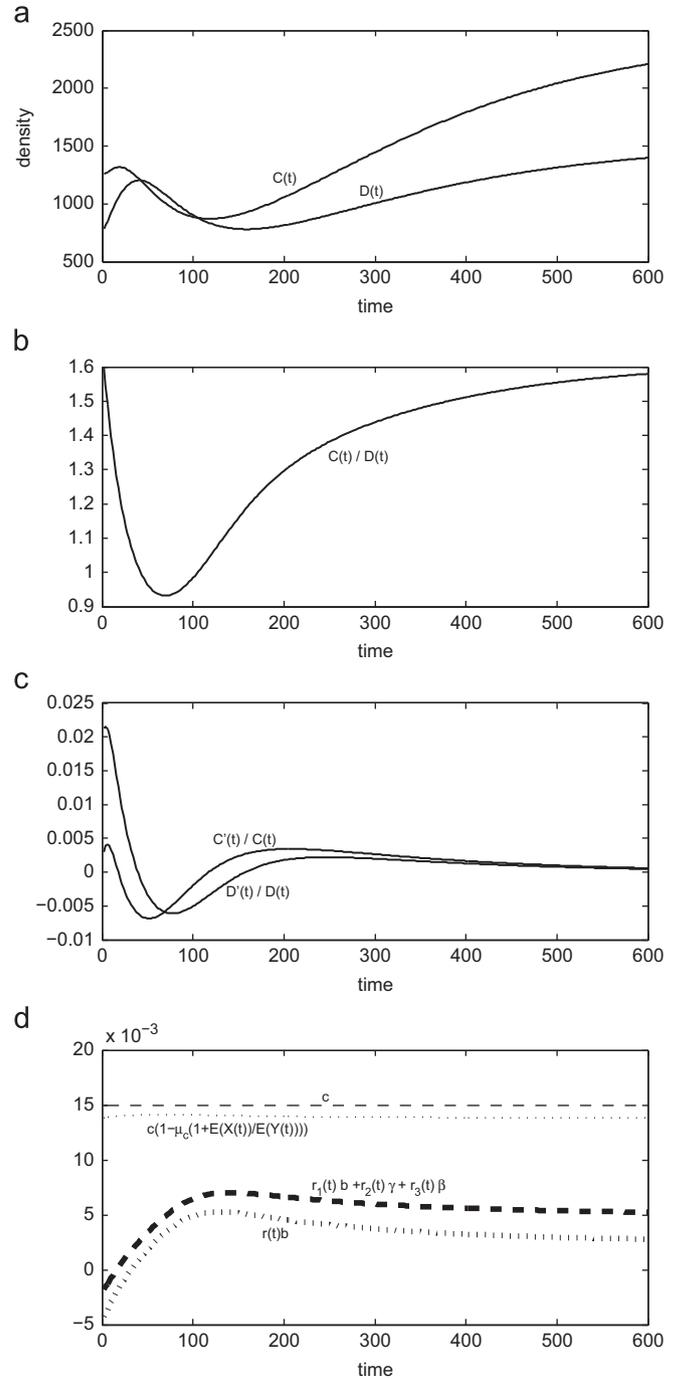


Fig. 2. Population dynamics for an example with individual-level and group-level events. The initial density distribution is $\theta_0(x,y) = \exp(-((x-40)^2 + (y-25)^2))$. In this example, the initial assortment is very unfavourable for cooperators. The density of cooperators in the population initially declines as the density of defectors increases, and at about $t=42.5$, the defectors overtake cooperators (a) however, since there are group-level events, the ultimate fate of cooperation cannot be reliably determined by only observing the initial population dynamics. To determine long-term dynamics, Eq. (12) must be solved. From (b) we see that in this example cooperation turns the tide at about $t=70.0$, and at about $t=105.2$ cooperators gain a majority which slowly grows as the population gradually reaches an equilibrium. (c) shows the left and right sides of (24). Comparison with panel (b) shows that (24) correctly predicts at each point in time whether cooperators or defectors are currently favored. (However, comparing (d) to panel (b) shows that the Hamilton rules (17) and (22) are of little use when group-level events occur.) As in Fig. 1, Hamilton’s rule does not correctly predict long-term dynamics. In particular, for $t < 70.0$, even the sophisticated version of Hamilton’s rule (24) is “unaware” that cooperation will successfully establish itself. The parameters for individual-level birth–death dynamics (7), (8) are $b=0.05$, $c=0.015$, $\beta=0.04$, $\gamma=0.0008$, $\mu_c=0.03$, $\mu_d=0.01$. The parameters for the group extinction rates (9) are $e_1=0.02$, $e_2=0.2$, $e_3=0.05$, the parameters for the group fissioning rate (10) are $f_1=0.0008$, $f_2=0.0016$, and the fissioning density is (11).

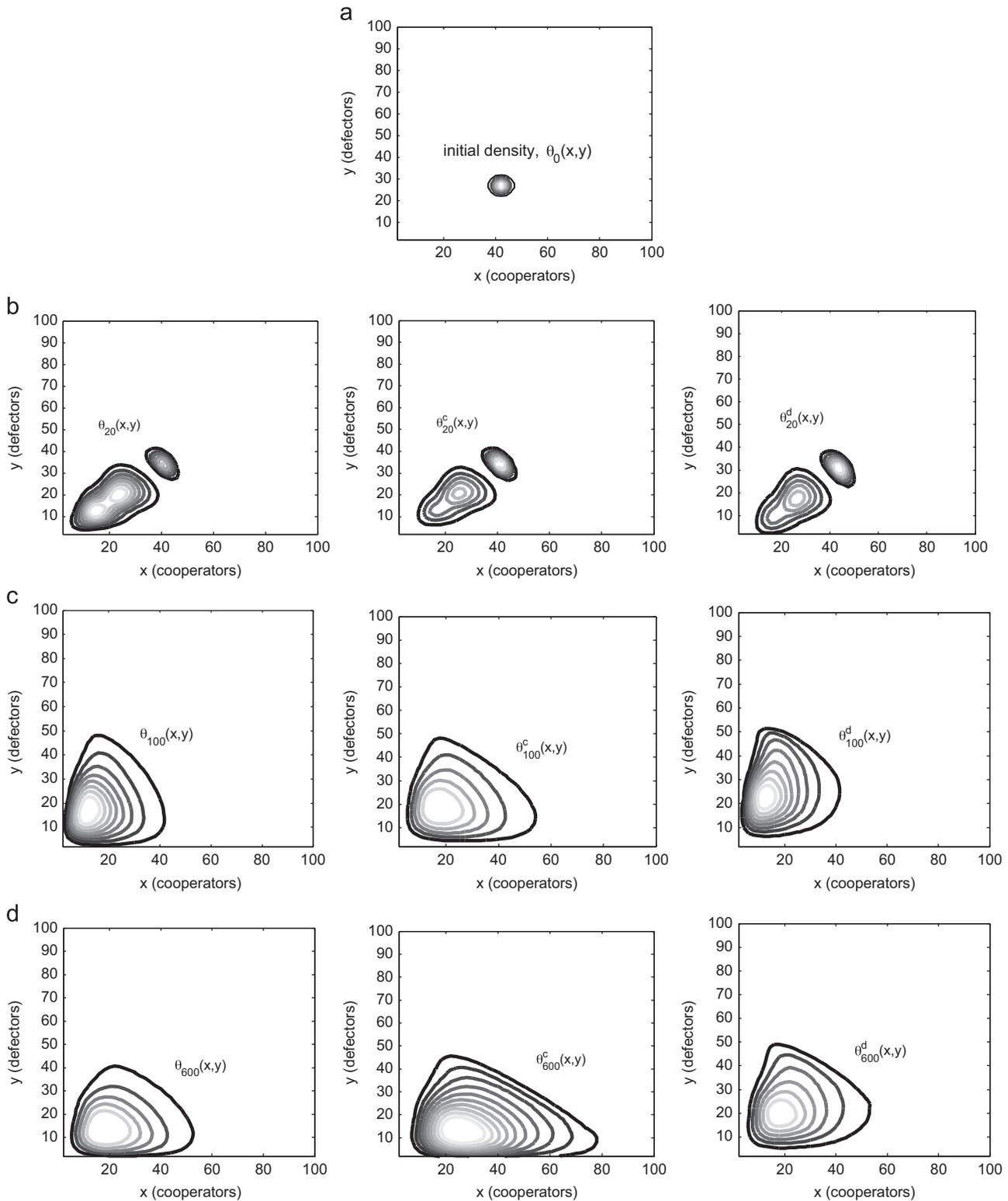


Fig. 3. The dynamics of cooperator–defector assortment. The scalar functions displayed in Fig. 2 were derived from $\theta_t(x,y)$, and in fact cannot be calculated any other way. There is much to be learned about the dynamics of assortment from $\theta_t(x,y), t \geq 0$, although it is difficult to display the entire function. The figure shows $\theta_t(x,y)$, $\theta_t^c(x,y)$, and $\theta_t^d(x,y)$ at times $t=0$ (initial condition), $t=20$, 100, and 600 for the same example as in Fig. 2. Panel (a) shows the initial distribution $\theta_0(x,y)$. By $t=20$ (row b), the shape of $\theta_{20}(x,y)$ shows the effects of the fissioning of some of the original groups. There is virtually no assortment at that time, and the cooperator-biased and defector-biased densities at $t=20$ show that there is not yet any significant assortment at that time. However, by $t=100$ the growth of the fissioned pieces has smoothed $\theta_t(x,y)$ so that it is unimodal, and $\theta_{100}^c(x,y)$ and $\theta_{100}^d(x,y)$ reveal a noticeable assortment, i.e., cooperators see a much more cooperative environment than defectors do. This assortment gradually increases over time, leading to an equilibrium population (approximated by $\theta_{600}(x,y)$) that contains a sizable fraction of large cooperative groups. Parameter values as in Fig. 2.

dynamics, see Fig. 1.) When group-level events can occur, the concept of individual-level “fitness” becomes more problematic. For example, if an individual resides in a group that is prone to

extinction (due, say, to the number of other groups in the environment) then its reproductive potential is diminished for reasons that have nothing to do with how it fares in the public

goods game it plays inside its group. On the other hand, an individual with low reproductive potential in its present group may suddenly find itself highly fit after a lucky fissioning event. In principle, all these possibilities can be averaged and a measure of “fitness” derived. However, there is no compelling reason to do this. The dynamical equations (12) and (13) can be solved without knowledge of the individual-level fitness measures, and in fact, the individual-level fitness measures can only be determined by first solving the dynamical equation.

It is impossible to derive a Hamilton-like condition for a model with group-level events that even superficially resembles the usual $rb > c$ form. However, using (21) we can derive a Hamilton-like rule for models with group-level events, as follows.

From (3) it follows that

$$C'(t) = \int \int x \frac{\partial \theta_t}{\partial t}(x,y) dy dx \quad \text{and} \quad D'(t) = \int \int y \frac{\partial \theta_t}{\partial t}(x,y) dy dx. \tag{23}$$

Substituting (12) into (23) yields the general Hamilton-like condition: cooperation is favored if

$$C^{-1} \int \int x \left(\rho(x,y) - (e(x,y) + f(x,y))\theta(x,y) - \frac{\partial[\theta\alpha_c]}{\partial x}(x,y) - \frac{\partial[\theta\alpha_d]}{\partial y}(x,y) \right) dy dx > D^{-1} \int \int y \left(\rho(x,y) - (e(x,y) + f(x,y))\theta(x,y) - \frac{\partial[\theta\alpha_c]}{\partial x}(x,y) - \frac{\partial[\theta\alpha_d]}{\partial y}(x,y) \right) dy dx. \tag{24}$$

Eq. (24) reduces to (22) if the rates that group-level events occur are set to zero, and reduces all the way to the standard Hamilton’s rule (17) if in addition there is no mutation and groups have fixed sizes (or more generally, if group-size determination of death rates is absent).

Fig. 2 shows the same information as Fig. 1, but for an example that includes group-level events. In this case the initial state of the population is unfavourable to cooperators, so their initial density plummets relative to the density of defectors (Fig. 2(a)). However, cooperators eventually turn the tide, and in equilibrium coexist with defectors. Fig. 2(b) shows the ratio of the densities of cooperators and defectors, and it is apparent that the point in time where cooperators are first favored is exactly when the two sides of (24) are equal (Fig. 2(c)). The generalized Hamilton’s rule reflects the instantaneous fate of cooperators at any point in time, but it cannot predict the long-term evolutionary dynamics. Note that at equilibrium, the generalized Hamilton’s rule (24) is an equality, because the fraction of cooperators does not change anymore. Note also that because of the presence of group-level events, the Hamilton’s rules (17), (20) and (22) do not even correctly predict the short-term dynamics (Fig. 2(d)).

4. The dynamics of assortment

The Hamilton-like inequalities derived in the previous section give conditions for cooperation to be favored, i.e., so that the fraction of cooperators increases, in a given population at a given point in time. If the condition is not satisfied then the fraction of cooperators decreases. In either case, a change in the fraction of cooperators causes a change in the state of the population, which in turn results in a change in the Hamilton-like inequalities. A prediction of that change is not provided by any of the rules derived in the previous section. In particular, the fact that cooperation is favored (or not favored) at one point in time is not a guarantee that it will always be, and hence these rules cannot predict the long-term dynamics of the system. The long-term dynamics, and in particular the resulting equilibrium distribution of cooperators and defectors, can only be determined by solving the appropriate dynamical equation (12) or (13).

Fig. 3 shows the dynamics of cooperator/defector assortment for the example of Fig. 2 by showing the densities $\theta_t(x,y)$, $\theta_t^c(x,y)$, and $\theta_t^d(x,y)$ at various points in time. Although the population

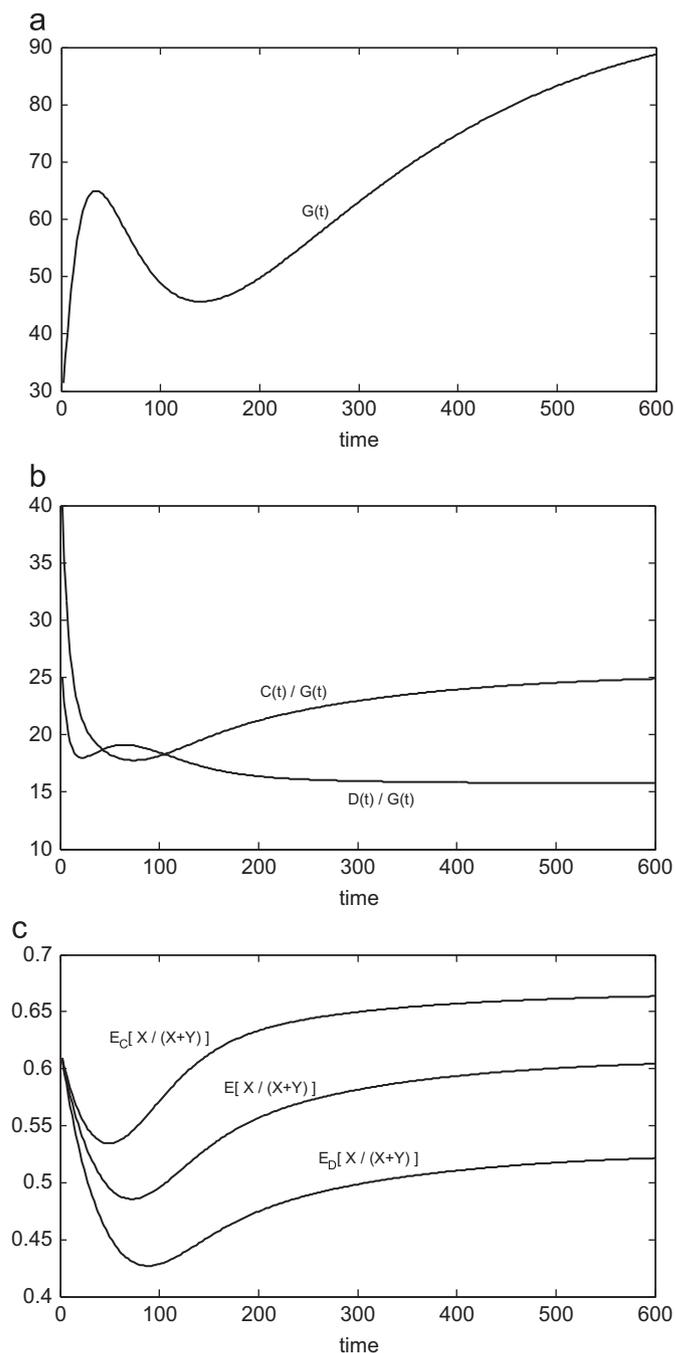


Fig. 4. Some group-level trait dynamics. Panel (a) shows how the number of groups in the population changes for the same example as in Figs. 2 and 3. At first the number of groups increases sharply as some of the original groups fission, but then the number declines as small groups go extinct. The numbers gradually recover as the population grows and becomes more cooperative. In (b) we see how the number of cooperators per group and defectors per group varies in time. In equilibrium, the average group has about 25 cooperators and 16 defectors, so cooperators make up more than 60% of the population. (c) shows the expected value of the fraction of cooperators, $X/(X+Y)$ as a function of time, as seen by a random cooperator, by a random individual, and by a random defector. The assortment produced by the interaction of group-level and individual-level events is clearly illustrated here. At first there is little or no assortment, as cooperators and defectors live in nearly identical groups with about 60% cooperators (see Fig. 3(a)). However, in equilibrium cooperators typically live in groups with more than 65% cooperators, while defectors typically live in groups that are barely half cooperators. Parameter values as in Fig. 2.

starts with very little assortment, as time goes on the average cooperator finds itself in a more cooperative group than defectors, and therefore cooperators experience a more cooperative interaction environment than defectors. The dynamics are further illustrated in Fig. 4, which again clearly reveals the importance of assortment (Fig. 4(c)).

Considering that in our model every group steadily becomes less cooperative over time, until cooperators are sustained in the population by mutation alone, the question is how cooperation is maintained at higher levels. When a group fissions, the resulting pieces are slightly different from each other since the individuals in the parent group “flip coins” to decide which piece to join. One piece will likely be more cooperative than the other, and will therefore grow faster. Furthermore, under reasonable assumptions (e.g. the example of Figs. 2–4), the more cooperative piece is less likely to die of extinction before growing large enough to fission itself. Thus, at the group-level, groups with a higher fraction of cooperators have a selective advantage. If this were the only selective force in play, the population would become predominantly cooperative, with defectors sustained by mutation alone. However, within the groups there is selective pressure against cooperators. The PDE (12) takes all these factors into account and predicts the resulting population dynamics. Over time, the evolution leads to an equilibrium population that contains both defectors and cooperators, living in a wide variety of group types (Fig. 3). The assortment that sustains cooperation at high levels can be seen clearly in Fig. 3(d), which shows the difference between the cooperator-biased and defector-biased equilibrium densities.

5. Conclusions

Hamilton’s rule $rb > c$ is often thought to be at the core of understanding the evolution of cooperation when cooperative individuals provide a benefit b to a public good at a cost c to self. We have derived generalized Hamilton’s rules for a two-level selection model, in which individuals are assumed to play public goods games in groups of various sizes. In contrast to many models in which the term group selection is colloquially used as referring to differential “productivity” among groups, and hence to the average fitness of individuals pertaining to a given group, our model is a true multi-level selection model, because it incorporates birth and death processes both at the individual and at the group-level (Okasha, 2006, Damuth and Heisler, 1988). In particular, groups are treated as units that can reproduce and die, and the dynamic variable that the model describes is the density of groups with different compositions of cooperators and defectors.

Generalized Hamilton’s rules can be derived for this model. However, even in the special case where the birth and death rates at the group level are 0, so that there are no group-level events, the generalized Hamilton’s rule (22) does generally not take the form $rb > c$. Such a form can only be achieved if demographic fitness effects (such as increased death rates in more crowded groups) are ignored or if these effects are nullified by constraining groups to all be the same size, in which case one obtains a classical Hamilton’s rule (17) where r is a measure of relatedness among those that interact cooperatively. However, this rule does not reflect the dynamics of cooperation in our model, precisely because demographic variability in individual death rates is not taken into consideration (Fig. 1). Moreover, even when all relevant rates are taken into account, the generalized Hamilton’s rules, i.e., (22) in the absence of group-level events and (24) in the presence of group-level events, can only predict the instantaneous dynamics of cooperation at any given point in time, but

cannot predict the long-term dynamics. In particular, these rules generally become equalities when the multi-level selection dynamics has reached equilibrium (Fig. 2). Thus, Hamilton-type rules are of very limited use for understanding the dynamics of cooperation in our multi-level selection model. In theory, it is always possible to extract some sort of Hamilton’s rule reflecting short-term dynamics of a given model, because such a rule is necessarily simply a reflection of model dynamics in terms of first derivatives, as e.g. given by (21) in the context of cooperators and defectors. However, even to predict such short-term dynamics, Hamilton’s rules should generally be expected to be complicated (e.g. (22)), and it is therefore often not clear what can be gained from emphasizing the formulation of such rules, especially since they do in general not give any information about the long-term dynamics of the system.

In general, the only way to preserve a simple form of Hamilton’s rule is to make post-hoc adjustments to the values of r , b , or c in order to give the correct “prediction.” But in this case the parameters of this simple form no longer represent measurable and discrete properties such as relatedness, and the benefit and cost of a cooperative act.

Our model has both similarities and differences with recent multi-level selection models. The model of Traulsen and Nowak (2006) also has birth and death processes at the individual level and group level, but unlike our model it has a fixed number of groups, a maximum group size, and discrete individuals. Their analysis focuses on relative fixation probabilities given no mutation, assumes rare group-level events, and includes homogeneous groups of cooperators unexposed to exploitation. Our results focus on the role of both individual-level and group-level events in the evolution of cooperation, and include mutation. van Veelen (2009) offers a useful framework for comparing different models, but in our model fitness effects depend on the density (not just the frequency) of cooperators and defectors. van Veelen (2009, 2011) confirms our result that Hamilton’s rule in its basic form does not correctly predict the direction of selection when fitness effects are non-additive, which is the case in our model when we include more realistic demographic forces beyond simple individual birth rates.

Depending on the parameters, our multi-level selection model considered here can produce different outcomes, but if cooperation is maintained, this always occurs because group-level events generate enough assortment between cooperative individuals (e.g. Fig. 3). Thus, to understand the evolution of cooperation in this model, one needs to understand the mechanisms by which fissioning and extinction of groups maintain a sufficient fraction of cooperative groups in the population. Hamilton’s rules neither shed any light on these mechanisms, nor on the dynamics of assortment, and instead are simply a reflection of the current state of the population.

Appendix

Here we show that it is possible to derive our Eq. (18) for the value of r in (17) starting with Hamilton’s covariance version of r (Hamilton, 1975), and using details of our model (without death processes and without group-level events). For more in-depth explorations of Hamilton’s rule, see e.g. van Veelen (2009, 2011). We use C and D for the total density of cooperators (as in (3)), and $Q = C/(C+D)$ for the overall fraction of cooperators. Our derivation is for a model with a finite number of possible group compositions, but our continuous model is easily recovered by taking a limit. Let K be the total number of different group compositions, indexed by k , and let $\hat{\theta}_k$ be the probability that a randomly chosen group is of the k th composition type, i.e., the fraction of groups

which contain x_k cooperators and y_k defectors. For example, there could be a group type corresponding to each point in the set $\{(iT/n, jT/n), 1 \leq i, j \leq n\}$ which (approximately) represents all (x, y) -groups with $x \leq T$ and $y \leq T$. In this case, $K = n^2$ and (by ordering the group types lexicographically) if $k = (i-1)n + j$ then $x_k = iT/n$ and $y_k = jT/n$. (Note that for space, compared to the text, we have dropped the (x, y) argument on $\hat{\theta}_k$ as well as the t subscript.) All the inputs for calculating r are taken at the same time.

We start with Hamilton's $r = Cov(G_A, G_O) / Var(G_A)$, where G_A is the frequency of the allele of interest in each potential actor (0 or 1 in a haploid model) and G_O is the average genotype of others the focal individual interacts with. In this case, G_O is just the frequency of cooperators in the focal individual's group. For a group composition k , this frequency is $q_k = x_k / (x_k + y_k)$. Note that the actor is included in the overall group frequency because this is a public goods game and some benefit feeds back to the actor (what Pepper (2000) calls "whole-group" altruism). Also note that in our model the frequency of cooperative acts is the same as the frequency of carriers of the cooperative genotype, but if cooperation was conditional or otherwise did not match the frequency of the genotype, then we would need to use Queller's version of r instead (Queller, 1985).

Normally, using the definitions of covariance and variance, we would sum over the whole population comparing each G_A and G_O with their overall mean values of Q . Given that we have the probability distribution of composition types, we can sum over these composition types instead of individuals, weighting each by its probability:

$$r = \frac{\sum_k \hat{\theta}_k [x_k(1-Q)(q_k-Q) + y_k(0-Q)(q_k-Q)]}{\sum_k \hat{\theta}_k [(1-Q)^2 + y_k(0-Q)^2]}$$

As an example, for a composition type k , each x_k cooperator contributes its covariance terms to the summation in the form $(G_A - E[G_A])(G_O - E[G_O]) = (1-Q)(q_k-Q)$, where $E[\dots]$ denotes the expected value, and similarly for the y_k defectors, and for calculating the variance in the denominator. By multiplying everything out, moving constants out of the summations, and then summing over each additive part separately, we get:

$$r = \frac{\sum_k \hat{\theta}_k [x_k q_k] - Q \sum_k \hat{\theta}_k [x_k] - Q \sum_k \hat{\theta}_k [x_k q_k] + Q^2 \sum_k \hat{\theta}_k [x_k] - Q \sum_k \hat{\theta}_k [y_k q_k] + Q^2 \sum_k \hat{\theta}_k [y_k]}{\sum_k \hat{\theta}_k [x_k] - 2Q \sum_k \hat{\theta}_k [x_k] + Q^2 \sum_k \hat{\theta}_k [x_k] + Q^2 \sum_k \hat{\theta}_k [y_k]}$$

We can now rewrite these summations as expectations, given that we are summing over a probability distribution. This yields:

$$r = \frac{E\left[X \frac{X}{X+Y}\right] - QE[X] - QE\left[X \frac{X}{X+Y}\right] + Q^2 E[X] - QE\left[Y \frac{X}{X+Y}\right] + Q^2 E[Y]}{E[X] - 2QE[X] + Q^2 E[X] + Q^2 E[Y]}$$

We can express Q also in terms of expectations as $E[X] / (E[X] + E[Y])$. By doing this and defining $s = E[X]$, $t = E[Y]$, $u = E[X^2 / (X + Y)]$ and $v = E[XY / (X + Y)]$, we get

$$r = \frac{u - \frac{s^2}{s+t} - \frac{su}{s+t} + \left(\frac{s}{s+t}\right)^2 s - \frac{sv}{s+t} + \left(\frac{s}{s+t}\right)^2 t}{s - 2\frac{s^2}{s+t} + \frac{s^3}{(s+t)^2} + \frac{s^2 t}{(s+t)^2}}$$

We now multiply out everything using a common denominator of $(s+t)^2$ in both numerator and denominator, and simplify as much as possible, which eventually yields

$$r = \frac{u}{s} - \frac{v}{t}$$

Substituting back for s , t , u , and v , respectively, this now matches Eq. (18) in the text as claimed.

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