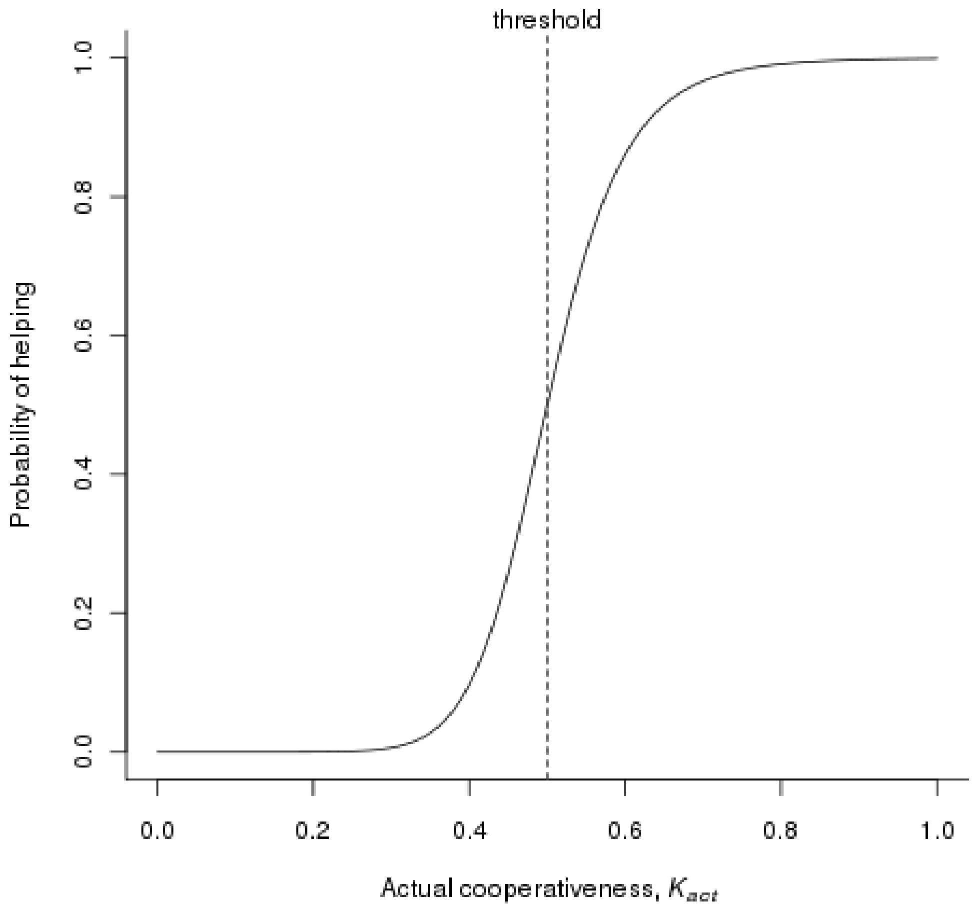
Electronic Supplementary Material to 'Cooperation among non-relatives evolves by state-dependent generalized reciprocity' by Zoltán Barta, John M. McNamara, Dóra B. Huszár, Michael Taborsky

ESM Fig. 1

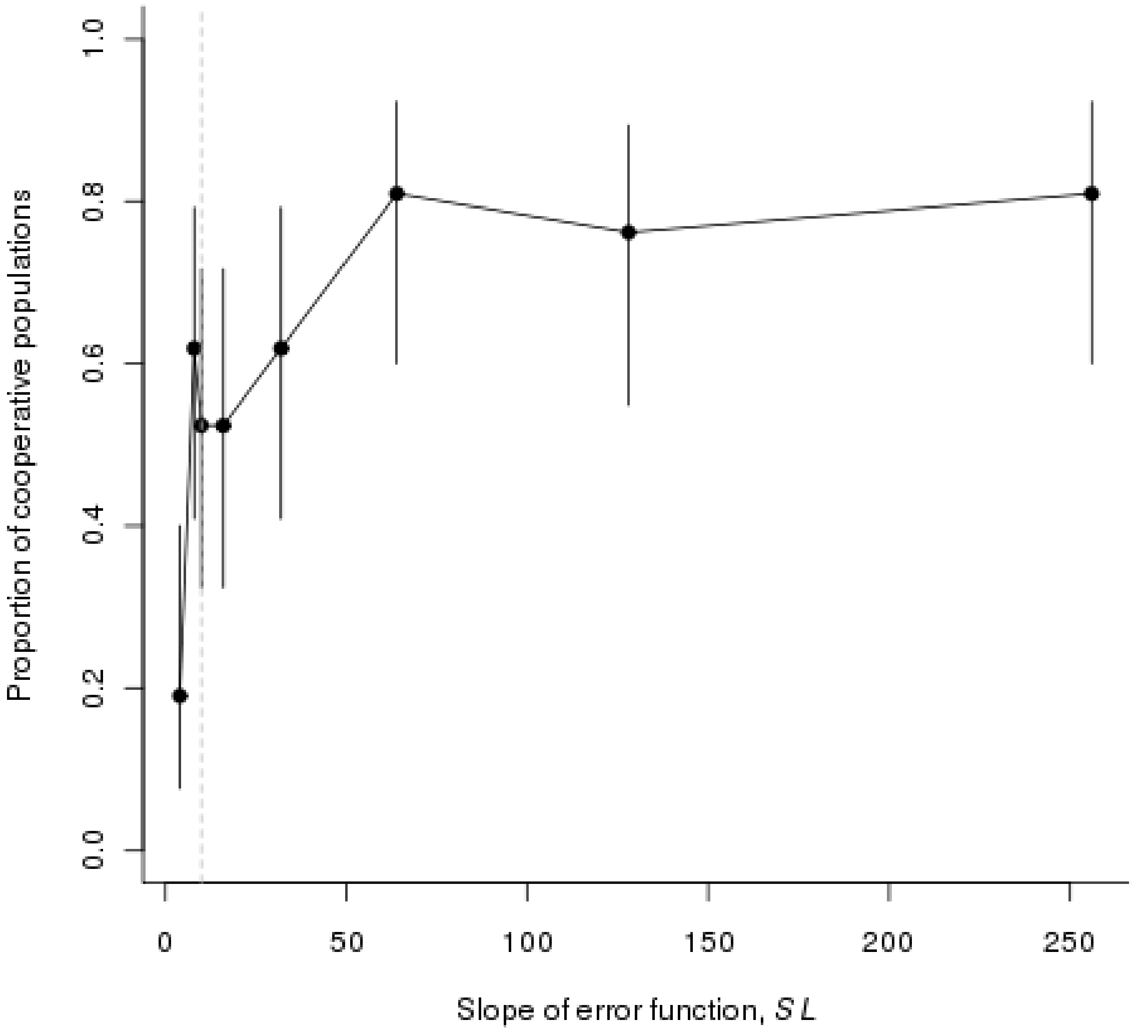


The probability of helping by an actor as the function of its internal state, the actual cooperativeness, K_{act}. The dashed line marks the threshold above which helping is more probable than defecting. The probability is given by the following function:

$$Pr(helping) = \frac{1}{1 + (K_{act} / TH)^{SL}},$$

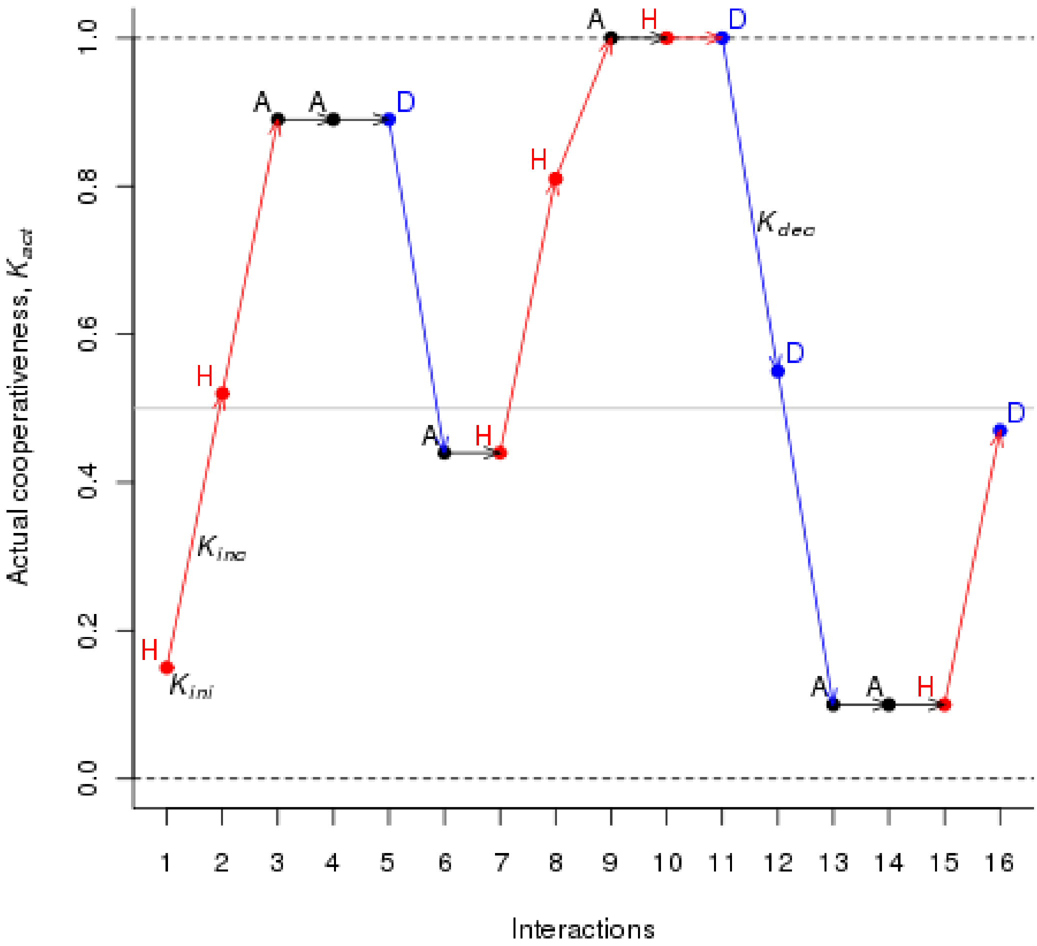
where TH is the threshold above which helping is more probable, while SL gives the level of error; the larger SL is, the smaller is the error.

ESM Fig. 2



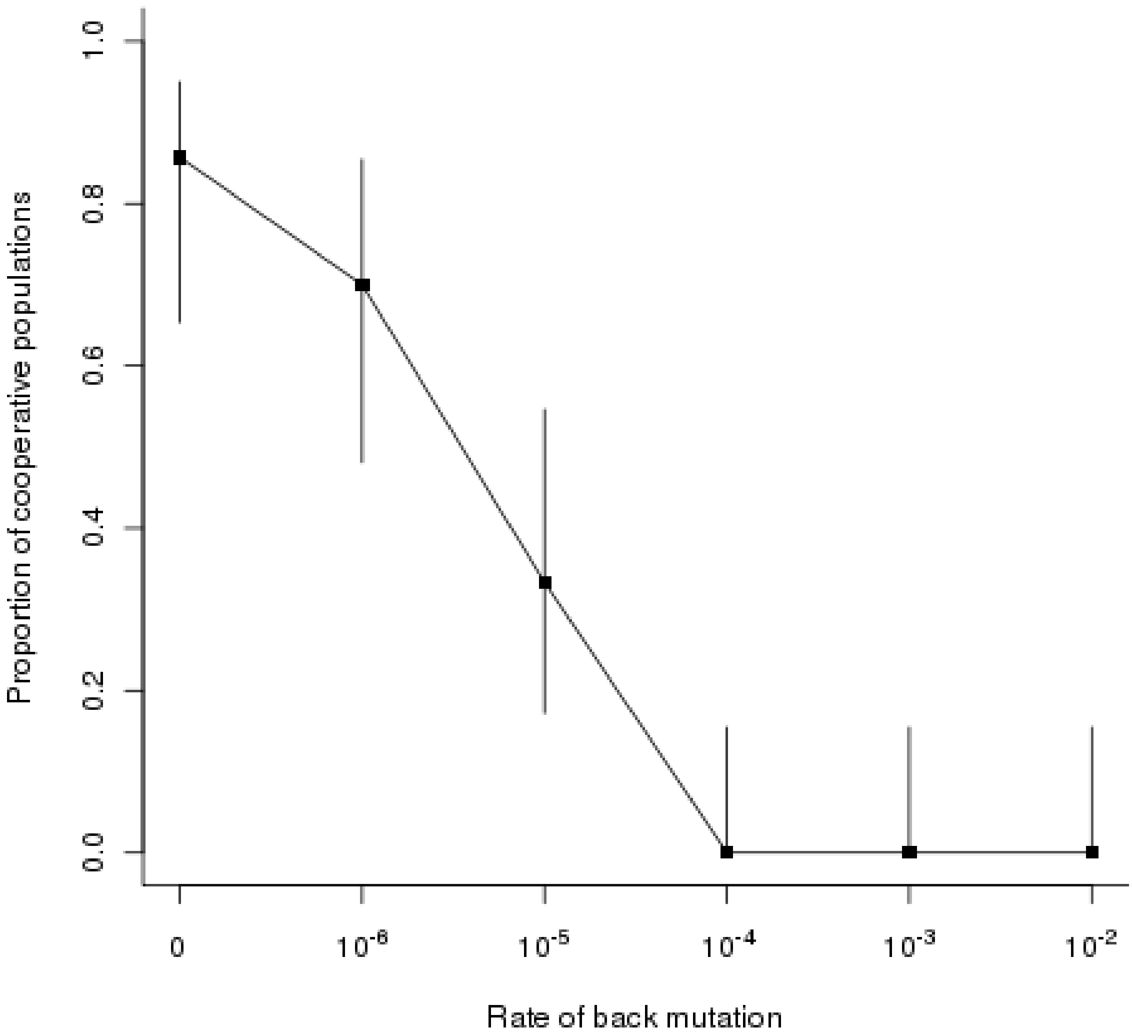
The effect of the level of error on the likelihood that cooperation evolves. Note the level of error increases from right to left, i.e. small value of *SL* means high error. The baseline level of error (used in all other computations) is marked by the vertical dashed line. As we used a rather large error, our results seem to be robust against changes in the level of error. Dots mark arithmetic means and vertical bars mark the 95% confidence intervals for binomial distributions.

ESM Fig. 3



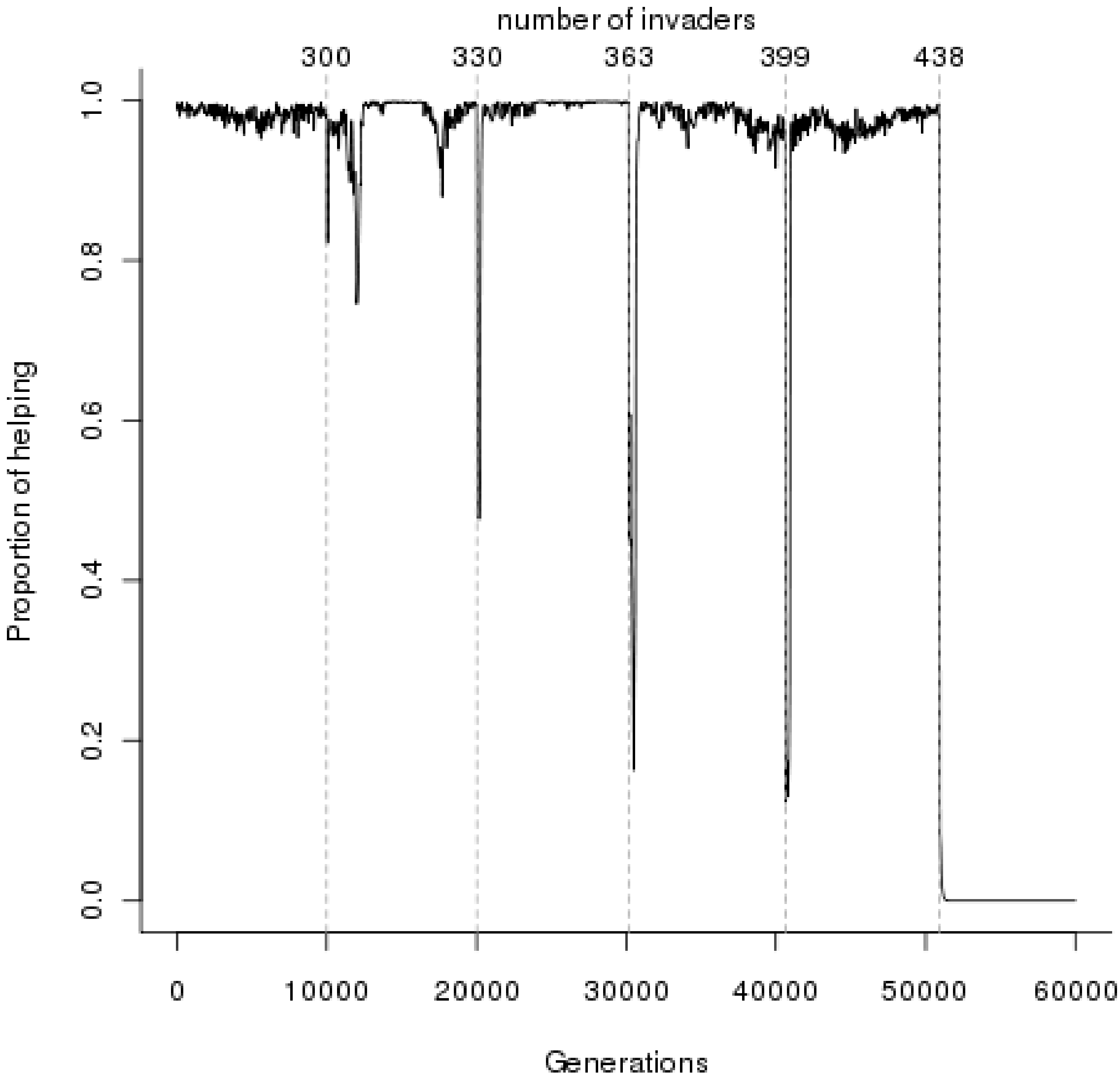
An exemplary trajectory of a focal individual's internal state variable, actual cooperativeness, K_{act}, over the interactions during a game. Black dots and “A”s mark when the focal individual plays actor in an interaction; in these cases its state does not change. Red dots and “H”s mark when it plays receiver and gets help; its state is then increased by K_{inc} (until $K_{act} \leq 1$). Blue dots and “D”s show when the focal player acts as receiver but does not get help; after this, its state is decreased by K_{dec} (until $K_{act} \geq 0$). Note, the actual cooperativeness can only change between zero and one. The figure was prepared with $K_{ini} = 0.15$, $K_{inc} = 0.37$ and $K_{dec} = 0.45$.

ESM Fig. 4



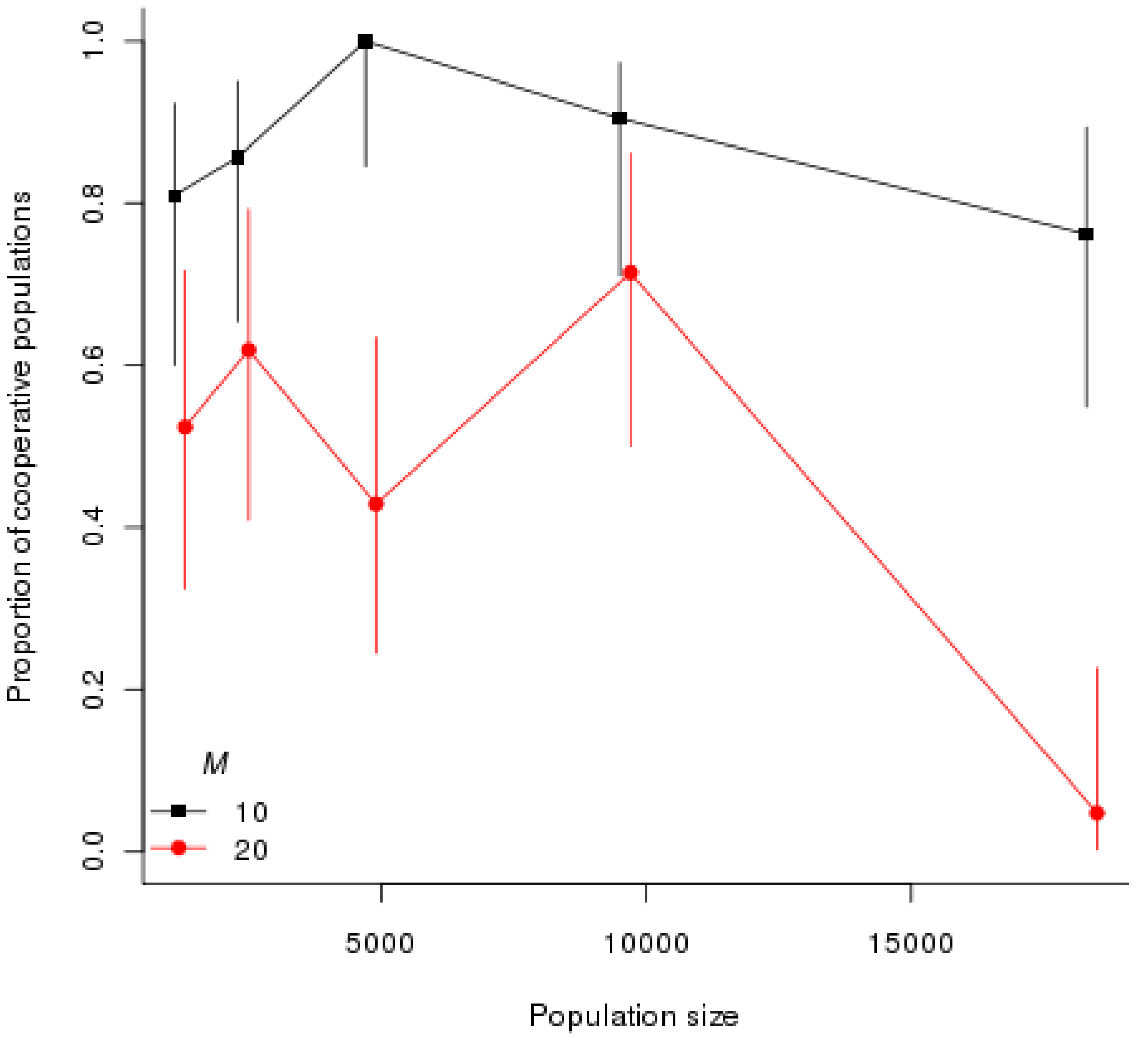
The effect of the rate of back mutation on the likelihood that cooperation evolves. When back mutation occurs, all alleles of an offspring (i.e. K_{ini}, K_{inc} and K_{dec}) are set to zero.

ESM Fig. 5



The proportion of helping in a cooperative population of 1200 individuals that is invaded consecutively by larger and larger numbers of unconditional non-cooperators (K_{ini} = 0, K_{inc} = 0, K_{dec} = 0). Vertical dashed lines mark the time of invasions, the number above them show the number of invaders.

ESM Fig. 6



The effect of population size on the likelihood that cooperation evolves for two different group sizes. The baseline population size is 1200 (the leftmost points). No clear trend emerges even as population size has been increased by 8-fold for $M = 20$ and by 16-fold for $M = 10$**.** Dots mark arithmetic means and vertical bars mark the 95% confidence intervals for binomial distributions.

ESM TEXT

Proofs for the simplified theoretical model

Assumptions

In this simplified model we are concerned with the spread of helping within a group of size M. We assume that there are n interactions, where in each interaction two randomly chosen individuals are paired. In this pairing one individual is assigned as the actor and the other as the recipient. The actor can either give help to the recipient or not. We assume that:

- At any time, each individual is in either one of two states, C (cooperator) or D (defector).
- In an interaction; if the actor is C then this individual gives help; if the actor is D then no help is given.
- If an individual is an actor in an interaction it retains its state in the next interaction.
- If an individual is a recipient in an interaction the state of the individual in the next interaction is C if help is received and is D if no help is received.
- The state of an individual that is not selected to interact does not change.

General questions

We investigate the quantities:
H_C = mean number of times an individual gives help, given initial state is C,
H_D = mean number of times an individual gives help, given initial state is D,
R_C = mean number of times an individual receives help, given initial state is C, and
R_D = mean number of times an individual receives help, given initial state is D.
We then use these results to see under what conditions an individual that is initially C in a group that is otherwise D gets a mean payoff that is positive.

Preparatory Result A

Consider a group in which individual i is initially C and individual j is initially D. Then, regardless of the starting states of others,
(a) P(individual i is C in interaction t) > P(individual j is C in interaction t),
(b) $H_C > H_D$, *and*
(c) $R_D > R_C$.

Proof of Preparatory Result A

In an interaction one of four possibilities occur; (i) individual i is chosen but not individual j, (ii) individual j is chosen but not individual i, (iii) both i and j are chosen, (iv) neither of i or j are chosen. It is easy to verify that in each case there is either no change to the state of either i or j, or else exactly one of i and j change state. In particular it is not possible for both to change state in the same interaction. Define the random variable T as follows. If neither i nor j change state over the n interactions set $T = n + 1$, else set T to be the number of the first interaction at which one of i or j changes state. Then i is in state C and j is in state D at the start of interactions 1, 2, …T, and i and j are in the same state at the start of interaction T+1.

Now consider the states of individuals i and j at the start of interaction t. In those cases where $t \leq T$ states have not changed so that i is in state C and j is in state D at the start of interaction t. Conversely, when $t > T$ the two individuals were in the same state on interaction T+1 and, by symmetry, the probabilities that each is in state C at the start of interaction t are equal. Thus averaging over possible values of T we have

P(individual i is C at the start of interaction t) > P(individual j is C at the start of interaction t).

This establishes part (a).

We now note that the probability that an individual gives help on an interaction is the probability that the individual is chosen as actor times the probability the individual is C. Thus

$$H_C = \frac{1}{M} \sum_{t=1}^{n} P(i \text{ is C at the start of round } t)$$
$$H_D = \frac{1}{M} \sum_{t=1}^{n} P(j \text{ is C at the start of round } t)$$

and (b) follows from part (a).

To prove part (c) we note that the probability of receiving help in an interaction is the probability of being chosen as recipient times the probability the chosen actor is C. Thus

$$R_C = \frac{1}{M} \sum_{t=1}^{n} p_i(t)$$
$$R_D = \frac{1}{M} \sum_{t=1}^{n} p_j(t)$$

where $p_k(t)$ denotes the proportion of the group other than individual k that are C at the start of interaction t. By part (a) $p_i(t) < p_j(t)$, so that (c) follows.

Proof of equation 1

We follow the fortunes of a specific individual over the n interactions. For this individual set

$h(t)$ = number of times the individual gives help on the first t interactions
$r(t)$ = number of times the individual receives help on the first t interactions
$I(t)$ = 0 if the state of the individual is D at the end of interaction t.
$I(t)$ = 1 if the state of the individual is C at the end of interaction t.

Let $Z(t) = h(t) - r(t) + I(t)$. We investigate $E\{Z(t+1)|Z(t)\}$.

Suppose first that the individual is not chosen in interaction t+1. Then $Z(t+1) = Z(t)$.

Now suppose that the individual is in state C at the start of interaction $t+1$ (i.e. $I(t) = 1$) and is chosen on this interaction.

- If the individual is assigned to be the actor then $h(t+1) = h(t) + 1$, $r(t+1) = r(t)$ and $I(t+1) = I(t)$. Thus $Z(t+1) = Z(t) + 1$.
- If the individual is assigned to be the recipient then $h(t+1) = h(t)$. There are two possibilities. If the actor helps then $r(t+1) = r(t) + 1$ and $I(t+1) = I(t)$. Thus $Z(t+1) = Z(t) - 1$. If the actor does not help then $r(t+1) = r(t)$ and $I(t+1) = 0 = I(t) - 1$. Thus again $Z(t+1) = Z(t) - 1$.

So, with probability 0.5 we have $Z(t+1) = Z(t) + 1$ and with probability 0.5 we have $Z(t+1) = Z(t) - 1$.

Now suppose that the individual is in state D at the start of interaction $t+1$ (i.e. $I(t) = 0$) and is chosen on this interaction.

- If the individual is assigned to be the actor then $h(t+1) = h(t)$, $r(t+1) = r(t)$ and $I(t+1) = I(t)$. Thus $Z(t+1) = Z(t)$.
- If the individual is assigned to be the recipient then $h(t+1) = h(t)$. There are two possibilities. If the actor helps then $r(t+1) = r(t) + 1$ and $I(t+1) = 1 = I(t) + 1$. Thus $Z(t+1) = Z(t)$. If the actor does not help then $r(t+1) = r(t)$ and $I(t+1) = I(t)$. Thus again $Z(t+1) = Z(t)$.

So, when the individual is D we have $Z(t+1) = Z(t)$.

Putting these cases together, we see that $E\{Z(t+1)|Z(t)\} = Z(t)$. Note this also holds for $t = 0$ if we set $Z(0) = I(0)$, where $I(0)$ indicates the initial state of the individual (0 if D, 1 if C). Thus the stochastic process $\{Z(t): t = 0, 1, 2, \ldots, n\}$ is a martingale. Thus by the martingale property $E\{Z(n)\} = Z(0)$. In particular

$$E\{h(n) - r(n) + I(n) \mid I(0) = 1\} = 1$$
$$E\{h(n) - r(n) + I(n) \mid I(0) = 0\} = 0$$

Note that $H_C = E\{h(n) \mid I(0) = 1\}$, $H_D = E\{h(n) \mid I(0) = 0\}$, $R_C = E\{r(n) \mid I(0) = 1\}$ and $R_D = E\{r(n) \mid I(0) = 0\}$. Furthermore, $E\{I(n)\}$ is the probability that the individual is in state C after all n interactions. Thus

$$H_C - R_C + \text{P(individual C after interaction } n \mid \text{initially C)} = 1$$
$$H_D - R_D + \text{P(individual C after interaction } n \mid \text{initially D)} = 0.$$

Subtracting these equations and using Preparatory Result A(a) we obtain

$$(H_C - H_D) + (R_D - R_C) < 1.$$

By Preparatory Result A(b)(c) $H_C - H_D > 0$ and $R_D - R_C > 0$. Thus

$$H_C - H_D < 1$$
$$R_D - R_C < 1,$$

and equation (1) (main text) follows.

Preparatory Result B

The expected total number of times that help is given in the n interactions is $(n/M)x_1$, where x_1 is the number of C initially present. As the average fitness increment in a group is $(b - c)(n/M)x_1$ the average fitness increases with x_1.

Proof of Preparatory Result B

Let $X(t)$ be the number of C individuals present at the start of interaction t. We first prove that the stochastic process $\{X(t)$: $t = 1, \ldots, n\}$ is a martingale.

Consider the pair formed in interaction t. There are 3 possibilities for this pair: we consider each in turn.

Both pair members are D. In this case both individuals are D in interaction t+1. Thus $X(t+1) = X(t)$.

One is D and the other is C. In this case if the actor is D both are D in the next interaction, while if the actor is C both are C. Since each is equally likely to be the actor we see that in interaction t+1, we have

- both are D with probability 0.5; i.e. $P(X(t+1) = X(t) - 1) = 0.5$
- both are C with probability 0.5; i.e. $P(X(t+1) = X(t) + 1) = 0.5$

Thus $E\{X(t+1)\} = X(t)$.

Both pair members are C. In this case both individuals are C in interaction t+1. Thus $X(t+1) = X(t)$.

Thus, whatever the configuration of the pair, the mean number of C individuals in the pair does not change. Thus we have the fundamental result that

$E\{X(t+1)\} = X(t)$,

i.e. the process $\{X(t))$ is a martingale. Thus

$E\{X(t)\} = x_1$ for all $t = 1, \ldots, n$,

where x_1 is the number of C present at the start of interaction 1. Since an individual is helped on interaction t if and only if the actor chosen is C, the probability an individual is helped is $E\{X(t)\}/M$. Thus the total number of helping acts performed in all n interactions has mean $(n/M)x_1$.

Proof of equation 2

When there is initially just one C individual, the average total number of times that help is given over the n interactions is $H_C + (M - 1)H_D$. By Preparatory Result B, this total also equals to n/M:

$H_C + (M - 1)H_D = n/M$.

By Preparatory Result A we have $H_C > H_D$. Thus

$MH_D < n/M$,

and hence

$H_D < n/M^2$.

Thus, by equation 1

$H_C < 1 + H_D < 1 + (n/M^2)$.

We now look at numbers receiving help. Since the total number of times that individuals receive help over the n interactions equals the total number of times help is given we have

$R_C + (M - 1)R_D = n/M$.

Since $R_C < R_D$ we can similarly derive

$R_D > n/M^2$.

By the martingale property, by equation 1

$R_C > R_D - 1 > n/M^2 - 1$.

Equation (2) then follows by the arguments in the main text.

Stability against invasion

As before there is a group of size M. There are n interactions, where in each interaction two randomly chosen individuals are paired. In this pairing one individual is assigned as the actor and the other as the recipient. The actor can either give help to the recipient or not. However, we now suppose that individuals can be of two sorts. An unconditional defector never gives help. A conditional cooperator behaves as follows:

- At a given time this individual is in either one of two states, C (cooperator) or D (defector).
- If the individual is an actor then help is given if the current state is C and no help is given if the current state is D.
- The state of an individual can only change when the individual is a recipient; after a round in which the individual is recipient the individual's state is C if help was received and is D if no help was received.

Before we looked at the situation where all individuals were conditional cooperators. Now we suppose that M-1 individuals are conditional cooperators – these are the resident strategists. The remaining individual will be referred to as the mutant. We will analyse whether the mutant does better to be an unconditional defector or a conditional cooperator.

We denote the number of the conditional cooperators that are in state C before the first round by x_1. We assume that $x_1 \geq 1$.

Payoff to the mutant as an unconditional defector

Suppose that the mutant is an unconditional defector. We evaluate the mean number of times this individual receives help given there is no limit on the number of rounds. This will then give an upper bound on the payoff to the mutant when the number of rounds is finite.

Let $X(t)$ be the number of individuals in state C just before round *t*. Suppose that $X(t)=x$. The various possibilities on round *t* are as follows.

- Resident C meets resident C. Then $X(t+1)=x$.
- Resident C meets resident D. Then $P(X(t+1)=x-1)=12=P(X(t+1)=x+1)$.
- Resident D meets resident D. Then $X(t+1)=x$.
- Mutant meets resident D. Then $X(t+1)=x$
- Mutant meets resident C. Then $P(X(t+1)=x-1)=12=P(X(t+1)=x)$.

The last of these possibilities occurs with probability $2\mathrm{x}/M(M-1)$. Thus, putting all the possibilities together we have

$$E\{X(t+1)|X(t)=x\}=x\left[1-\frac{1}{M(M-1)}\right].$$

Thus since $E\{X(t+1)\}=E\{E\{X(t+1)|X(t)\}\}$ we have

$$E\{X(t+1)\}=\left[1-\frac{1}{M(M-1)}\right]E\{X(t)\}.$$

Iterating this formula then gives

$$E\{X(t)\}=\left[1-\frac{1}{M(M-1)}\right]^{t-1}x_1 .$$

Thus

$$\sum_{t=1}^{\infty}E\{X(t)\}=M(M-1)x_1 . \qquad (1)$$

Now if $X(t)=x$ the probability that the mutant will receive help in round *t* is $x/M(M-1)$. Thus, averaging over values of *x*, the probability of receiving help on round *t* is $E\{X(t)\}/M(M-1)$. Thus by equation (1), the mean total number of times the mutant receives help over an infinite number of rounds is x_1 . The payoff to the mutant when there is a finite number of rounds is thus less than $x_1 b$.

Payoff to the mutant as a conditional cooperator

Suppose now that the mutant is a conditional cooperator with initial state D. Then, all individuals are conditional cooperators, with x_1 initially in state C and $M-x_1$ initially in state D. By preparatory result B over *n* rounds help is given on average $(n/M)x_1$ times. Thus

$$x_1 H_C+(M-x_1)H_D=(n/M)x_1 .$$

By preparatory result A $H_D<H_C$. Thus

$$H_D < \frac{n}{M^2} x_1 \ .$$

Since the number of times that help is received equals the number of times help is given we also have

$$x_1 R_C + (M - x_1) R_D = (n/M) x_1$$

By preparatory result A $R_C < R_D$. Thus

$$R_D > \frac{n}{M^2} x_1 \ .$$

The payoff to the mutant is $bR_D - cH_D$. Thus this payoff is greater than

$$(b-c) \frac{n}{M^2} x_1 \ .$$

Stability against invasion

From the above the resident strategy of conditional cooperation is stable against invasion by a mutant playing unconditional defection if

$$(b-c) \frac{n}{M^2} x_1 > x_1 b \ .$$

Assuming that $b > c$, this holds provided that

$$n > M^2 b / (b-c) \ .$$

Intuitively, if the mutant is an unconditional defector then cooperation eventually ceases in the group. There is thus an upper bound of $x_1 b$ on the payoff to the mutant no matter how many rounds are played. If instead the mutant is a conditional cooperator then there are two possibilities in the long term; eventually all group members are C or eventually all group members are D. Averaging over these possibilities the payoff to the mutant increases essentially linearly with *n* for large *n*. Thus if there is a sufficient number of rounds the mutant does better as a conditional cooperator.