Supplementary Information: The coevolution of cooperation and cognition in humans

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Contents

1 Demography and cognition

In this section, we derive the fitness of a focal individual under the modified life cycle with dispersal and overlapping generations. The changes to our baseline model in the main text are as follows. After the social interactions, adults on patches produce a very large number of juveniles who each disperses with probability m to some new random patch (excluding the natal patch). On each patch, adults survive to the next generation with probability s, in which case they remain on their patch. Juveniles compete for the empty spots until patches reach size n. The remaining juveniles die. Therefore, the fitness of a focal individual i is given by

$$w_i = s + (1 - s)\left[\frac{(1 - m)F_i}{(1 - m)F' + m\bar{F}} + \frac{mF_i}{\bar{F}}\right], \tag{S1}$$

where $F_i = 1 - x_0 c - y_0 d + B(x_g, y_g)$ is the fecundity of the focal individual i, and x_0 and y_0 are the focal's cooperation and cognition traits, respectively; $F' = 1 - x_g c - y_g d + B(x_g, y_g)$ is the average fecundity of individuals on the focal individual's patch (including the focal), and $\bar{F} = 1 - \bar{x}c - \bar{y}d + B(\bar{x}, \bar{y})$ is the average fecundity of the population.

With this life cycle, the whole-group relatedness is given by

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$$R = \frac{1+s}{1 + 2m(n-1) - m^2(n-1)(1-s) + s}. \tag{S2}$$

Then, by substituting Eq.(S1) and Eq.(S2) into the expression for the selection gradient in the main text (methods), and finding when the selection gradients are positive, we obtain Ineq.(3) of the main text, where R_o is replaced by

$$\kappa = \frac{2(1-m)s}{n[2 - m(1-s)] + 2(1-m)s}. \tag{S3}$$

Here, κ is the scaled relatedness coefficient which is demographically scaled so as to capture the effect of both increased genetic assortment and increased local competition between kin (Lehmann and Rousset, 2010). Increasing survival s increases κ (so $\mathrm{d}\kappa/\mathrm{d}s > 0$), and increasing both dispersal m and patch size n decrease κ (so $\mathrm{d}\kappa/\mathrm{d}m < 0$, and $\mathrm{d}\kappa/\mathrm{d}n < 0$). Therefore, a decrease in scaled relatedness can occur whenever survival decreases, or if either patch size and dispersal increases. Note that the maximum value that κ can take with this specific life cycle is $1/(n+1)$, i.e. when $s \to 1$ and $m \to 0$. Therefore, the relevant area of parameter space for the emergence of cooperation and cognition in this life cycle is between $\kappa = 0$ and $\kappa = 1/(n+1)$. In the absence of survival ($s \to 0$), scaled relatedness becomes 0, and so we recover the cancellation result that cooperation can only be favoured through direct fitness benefits in Wright's island model (Taylor (1992); Taylor and Irwin (2000); Table S1).

2   Computer simulations

We use individual-based computer simulations to confirm our analytical prediction on the stability of fully cooperative and cognitively enhanced populations. We model a finite population subdivided into n_p patches, each of size n. Individuals are haploid and generations are non-overlapping.

The life-cycle is as follows: (i) each patch is colonised by exactly k founding individuals. (ii) Founders produce a very large number of juveniles, who compete for space on the patch. Exactly n randomly selected juveniles survive, and the founders die. (iii) Social interactions occur between juveniles within patches. (iv) Juveniles reach adulthood and produce a very large number of offspring, proportionally to the payoffs acquired during social interactions. All offspring migrate to a global pool, with complete mixing. (v) Exactly kn_p individuals are randomly selected from this global pool to be the founders for step (i). Rather than modeling a life-cycle that closely resembles that of early human groups, we chose this particular life-cycle because it allows us to easily vary scaled relatedness between patch members, which tends to $\kappa = 1/k$ when n_p is large, while maintaining patch size n constant.

As in our analytical model, individuals carry two continuous traits: a cooperation trait x and a cognition trait y, coding for the probability of contributing to a public good and developing cognition, respectively. Social interactions are described in the main text. Random numbers were generated in order to determine who cooperated and/or developed cognition. Then, the payoff from the game to a focal individual i in a given group was calculated in the following way.

$$\Pi_i(N_c, N_{cog}) = -cx_1 - dy_1 + N_c\frac{b}{n} + N_{cog}\frac{b + b_C}{n}\exp\left[\alpha\frac{N_{cog} - 1}{n}\right], \qquad \text{(S4)}$$

where x_1 and y_1 are discrete variables determining whether or not the focal individual cooperated and developed cognition, respectively. Both N_c and N_{cog} are the total number of cooperators and cognitively enhanced cooperators in the focal individual's group, respectively. Note that the total number of cognitively enhanced cooperators was corrected to avoid a single cognitively enhanced cooperators producing synergistic benefits. In order to avoid negative payoffs, an amount $1 + c + d$ was added to all individuals.

Then, for the colonisation phase, founders were randomly sampled among the previous generation of juveniles, proportionally to their relative payoffs (i.e., focal payoff/sum of all payoffs). Mutations could occur during reproduction in step (ii). Specifically, in each of the n juveniles, each trait had a mutation probability $\mu = 0.01$, in which case the current trait value was incremented by a normally distributed random number with mean 0 and variance $\sigma = 0.01$.

All simulations were run for 10^6 generations. Half-way through, the number of founders k, was reduced to $k = 100$, in order to decrease relatedness.

Simulation results are presented in Fig.S6 - S8. We found that simulation runs where cognition was not allowed to evolve could never maintain cooperation levels (Fig.S6). However, cooperation could be maintained when cognition was allowed to evolve, provided it enabled individuals to (i) produce sufficiently larger benefits, and (ii) generate synergistic benefits (Fig.S7 - S8).

3 Machiavellian cognition

In this section, we present the conditions for cooperation and cognition to be favoured when cognition enables individuals to exploit their less intelligent patch members. Using the benefit production function used in the main text (methods; Fig. 1 of the main text) with the new benefit received by a focal individual $B(x_g, y_g)(1 + gy_0)/(1 + gy_g)$, substituting into the expressions for the selection gradients (main text) and replacing R with $1/n + R_o(n-1)/n$, we find that $H(x, y) > 0$ and $K(x, y) > 0$ if

$$[1 + (n - 1)R_o]\left(\frac{b}{n}(1 - y) + y\frac{b + b_C}{n}e^{\alpha y}\right) > c \qquad \text{(S5a)}$$

$$x\left\{[1 + (n - 1)R_o]\left(\frac{b + b_C}{n}e^{\alpha y}(1 + \alpha y) - \frac{b}{n}\right) + \frac{g}{1 + gy}(n - 1)(1 - R_o)\left(\frac{b}{n}(1 - y) + \frac{b + b1}{n}e^{\alpha y}y\right)\right\} > d. \qquad \text{(S5b)}$$

We first consider the initial emergence of cooperation and cognition, assuming no cognition in the population (i.e., $y \to 0$). As in our baseline model, cooperation will be favoured if $(n - 1)R_ob/n > c - b/n$, and cognition will favoured only if

$d < 0$. Then, assuming cooperation is favoured and evolves in the population, cognition will invade from rarity as soon as cooperation reaches a threshold level $x^* = dn/\{b_C + (n-1)[bg(1-R_o) + b_C R_o]\}$. Assuming cooperation has fully invaded before cognition initially evolves (i.e. $x \to 1$ and $y \to 0$), then cognition will be favoured if $bg + [1 + (n-1)R_o](b_C - bg)/n > d$.

Here, relatedness can have a negative impact on the selection pressure on Machiavellian cognition (i.e. dK/dR_o can be negative). This can be seen from Eq.(S5b), where the benefits from the public good are multiplied by $1 - R_o$, so that increasing R_o decreases the benefit from exploiting others. An intuitive explanation for this result is that a focal individual is only able to exploit partners who have a lower cognition level. By increasing relatedness, social partners become more and more alike, and so receive fewer and fewer benefits from exploiting others. Furthermore, if cognition does not enable individuals to generate larger benefits ($b_C = 0$), then cognition can invade from rarity if $x(n-1)(1-R_o)gb/n > d$, and so R_o completely hinders the evolution of cognition. More formally, the derivative of the selection gradient on cognition with respect to R_o will be negative (i.e. $dK/dR_o < 0$) if, and only if

$$(b + b_C)e^{ay}[1 + ay(1 + gy)] < b(1 + g). \tag{S6}$$

So, if $b_C, \alpha = 0$, Ineq.(S6) always holds if $g > 0$.

Nevertheless, if cognition allows for larger benefits and synergism, the condition for cognition to invade from rarity is less stringent than in our baseline model, as it now depends also on the baseline benefit b and g (Fig. S9). So, both larger b and g favour the evolution of cognition.

We present in Table (S2) the conditions for full cooperation and Machiavellian cognition to remain stable in the absence of relatedness ($H(1,1) > 0$ and $K(1,1) > 0$ with $R_o = 0$). We can see that allowing cognitive individuals to exploit their partners does not alter the selection gradient for cooperation, which remains the same as in our baseline model. However, the condition for cognition to be stable is now less stringent than before. Cognition can now be stable even in the absence of both larger benefits and synergism ($b_C, a = 0$). This is not surprising, because in a population with full cooperation and cognition, a focal mutant with a lower level of cognition will get exploited by its partners who will take some of its share from the public good.

4 Supplementary tables and figures

b_C	α	$H > 0$		$K > 0$
$= 0$	$= 0$	$\dfrac{b}{n} > c$		$0 > d$
> 0	$= 0$	$\dfrac{b + b_C}{n} > c$		$\dfrac{b_C}{n} > d$
$= 0$	> 0	$e^\alpha \dfrac{b}{n} > c$	$e^\alpha(1 + \alpha)\dfrac{b}{n} - \dfrac{b}{n} > d$	
> 0	> 0	$e^\alpha \dfrac{b + b_C}{n} > c$	$e^\alpha(1 + \alpha)\dfrac{b + b_C}{n} - \dfrac{b}{n} > d$	

Table S1: Conditions for full cooperation and full cognition to be favoured in the absence of relatedness ($R_o = 0$), i.e., $H(1,1) > 0$ and $K(1,1) > 0$.

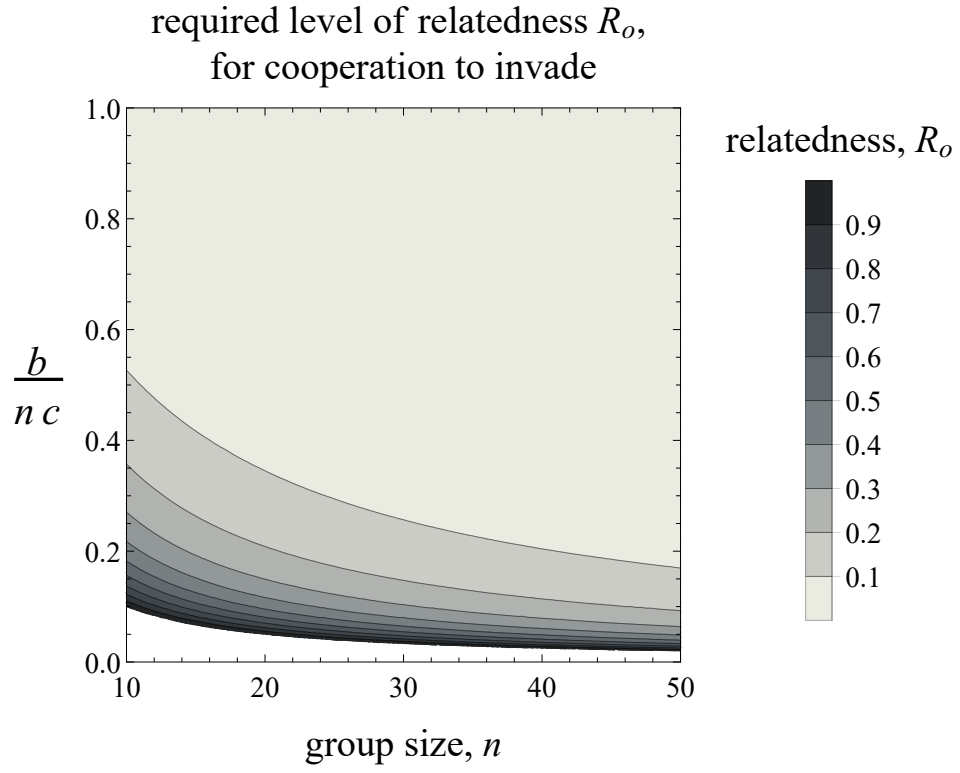| b_C	α	$H > 0$	$K > 0$
$= 0$	$= 0$	$\dfrac{b}{n} > c$	$\dfrac{b}{n}(n-1)\dfrac{g}{1+g} > d$
> 0	$= 0$	$\dfrac{b+b_C}{n} > c$	$\left(\dfrac{b_C}{n} + g\left[\dfrac{b}{n}(n-1) + b_C\right]\right)\dfrac{1}{1+g} > d$
$= 0$	> 0	$e^\alpha\dfrac{b}{n} > c$	$e^\alpha\dfrac{b}{n}\left(\dfrac{1+gn}{1+g} + a\right) - \dfrac{b}{n} > d$
> 0	> 0	$e^\alpha\dfrac{b+b_C}{n} > c$	$e^\alpha\dfrac{b+b_C}{n}\left(\dfrac{1+gn}{1+g} + a\right) - \dfrac{b}{n} > d$

Table S2: Conditions for full cooperation and full Machiavellian cognition to be favoured in the absence of relatedness ($R_o = 0$), i.e., $H(1,1) > 0$ and $K(1,1) > 0$.

required level of relatedness R_o,
for cooperation to invade

Figure S1: Invasion and stability conditions for cooperation. Parameter space where full cooperation is stable (and can invade) without cognition ($H(0,0) > 0$), as a function of group size and the per capita share to cost ratio from cooperation (scaled by group size n).
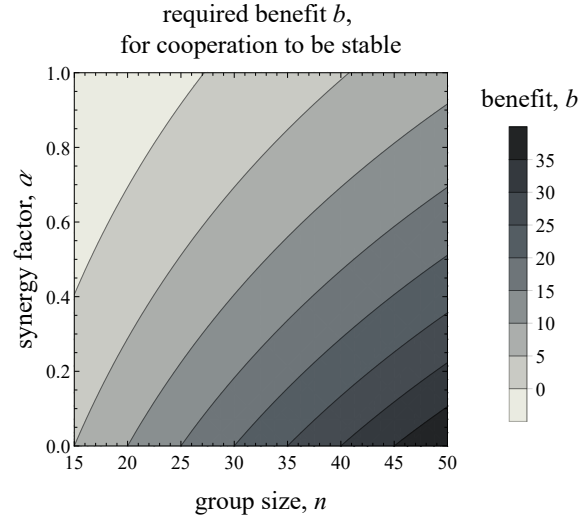
required benefit b,
for cooperation to be stable

Figure S2: Stability conditions for cooperation in the absence of relatedness. Parameter space where full cooperation is stable with full cognition ($H(1,1) > 0$ and $K(1,1)$), as a function of group size and the synergy factor α. Parameters: $c = 1$, $d = 1$, $b_C = 10$, $R_o = 0$.
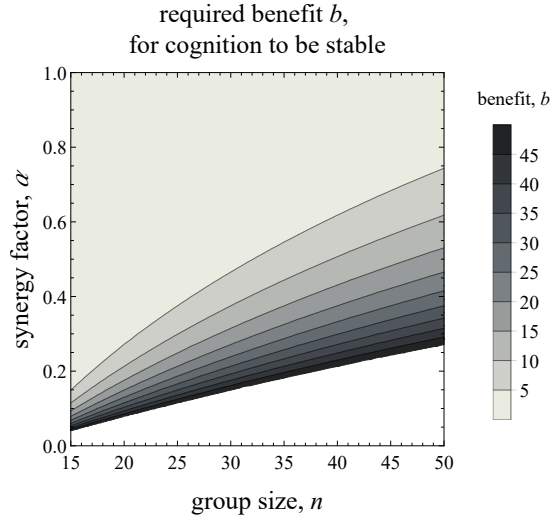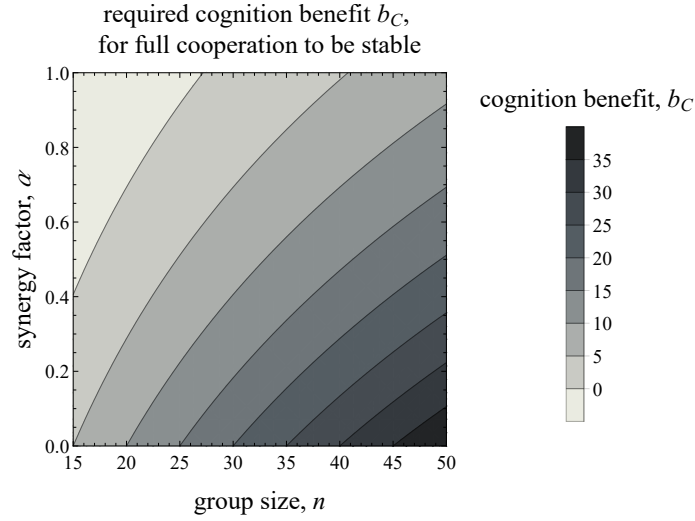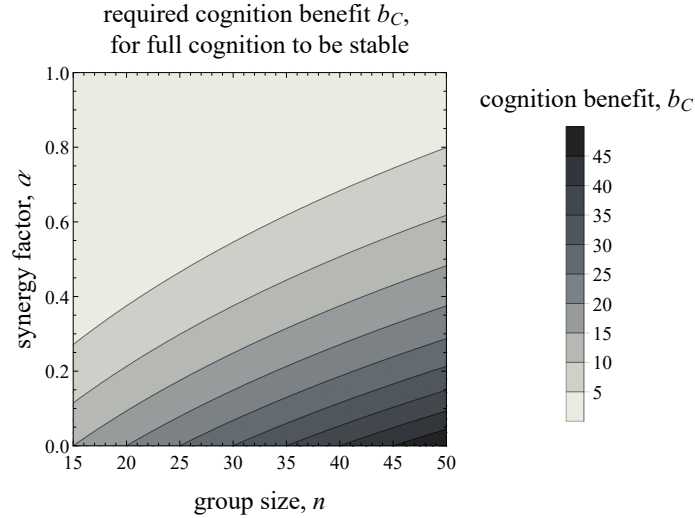

required benefit b,
for cognition to be stable

Figure S3: Stability conditions for cognition in the absence of relatedness. Parameter space where full cognition is stable with cooperation ($H(1,1) > 0$ and $K(1,1) > 0$), as a function of group size and the synergy factor α. Parameters: $c = 1$, $d = 1$, $b_C = 10$, $R_o = 0$.

required cognition benefit b_C,
for full cooperation to be stable

cognition benefit, b_C

Figure S4: Stability conditions for cooperation in the absence of relatedness. Parameter space where full cooperation is stable with full cognition ($H(1,1) > 0$ and $K(1,1) > 0$), as a function of group size and the synergy factor α. Parameters: $c = 1$, $d = 1$, $b = 10$, $R_o = 0$.

required cognition benefit b_C,
for full cognition to be stable

cognition benefit, b_C

Figure S5: Stability conditions for cognition in the absence of relatedness. Parameter space where full cognition is stable with full cooperation ($H(1,1) > 0$ and $K(1,1) > 0$), as a function of group size and the synergy factor α. Parameters: $c = 1$, $d = 1$, $b = 10$, $R_o = 0$.
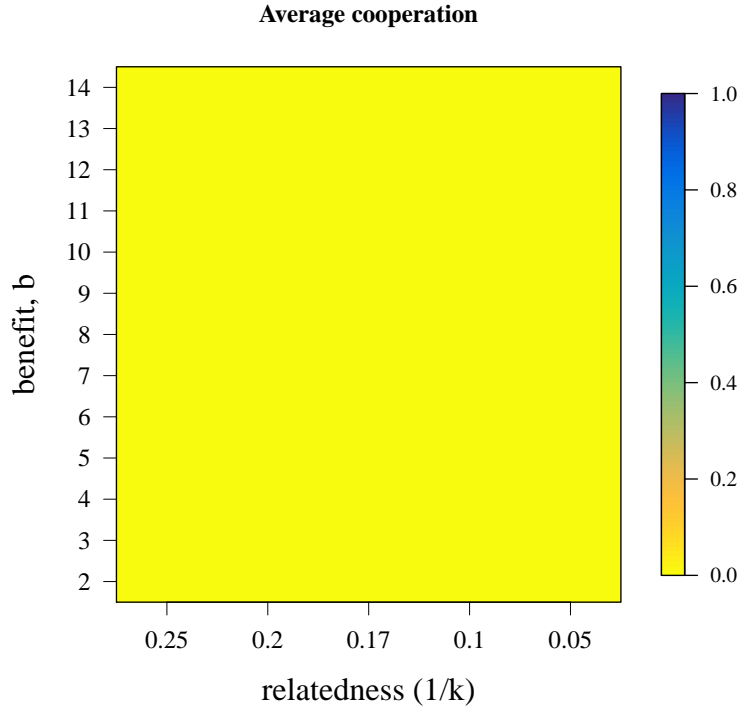
Figure S6: Cooperation strategy x at the end of simulation runs without cognition. Simulations were started with different relatedness values (x axis) for different values of benefit b. Half-way through, relatedness was decreased to $R_o = 0.01$ (i.e., $k = 100$). Parameters: $n = 15$, $c = 1$, $\mu = 0.01$, $\sigma = 0.01$
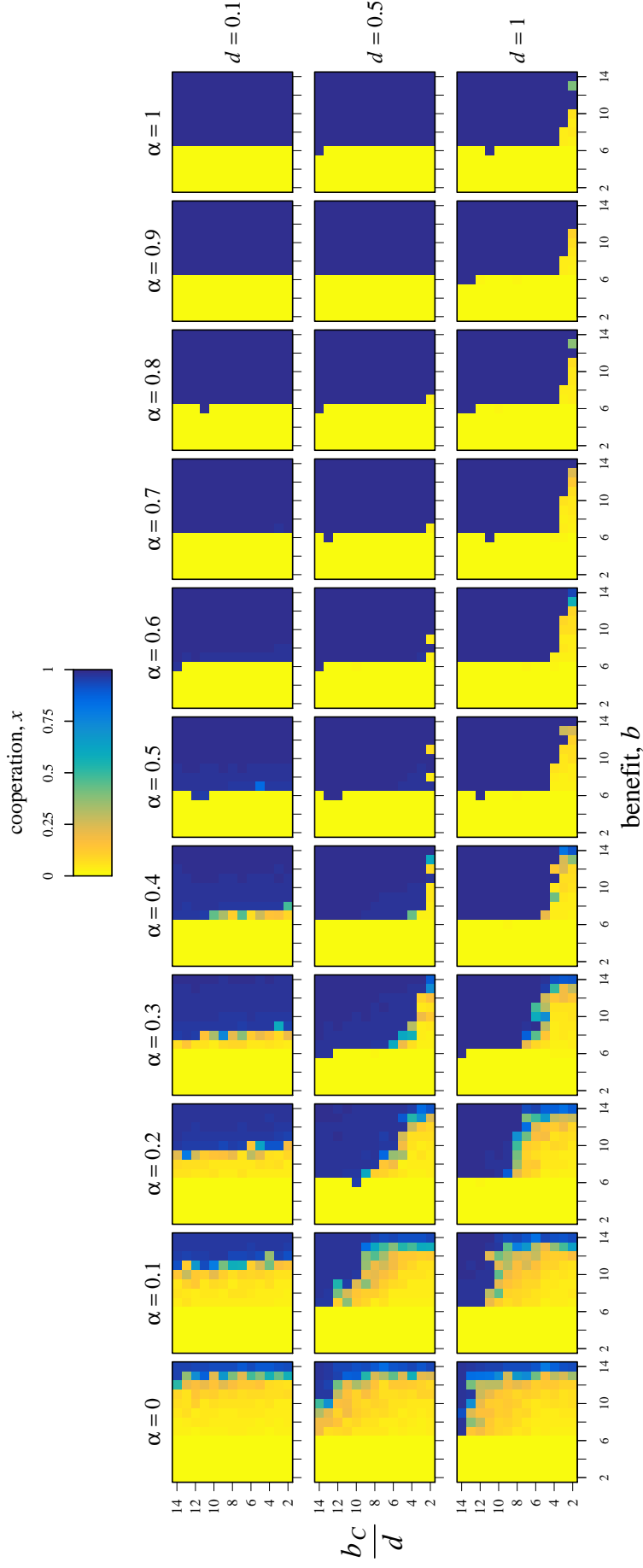
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Figure S7: Cooperation strategy x at the end of simulation runs with cognition and $k = 10$. Simulations were started with relatedness $R_o = 0.1$ ($k = 10$) for different values of benefit b, cognition benefit to cost ratio b_C/d and synergy factor α. Half-way through, relatedness was decreased to $R_o = 0.01$ (i.e., $k = 100$). Parameters: $n = 15$, $c = 1$, $\mu = 0.01$, $\sigma = 0.01$.
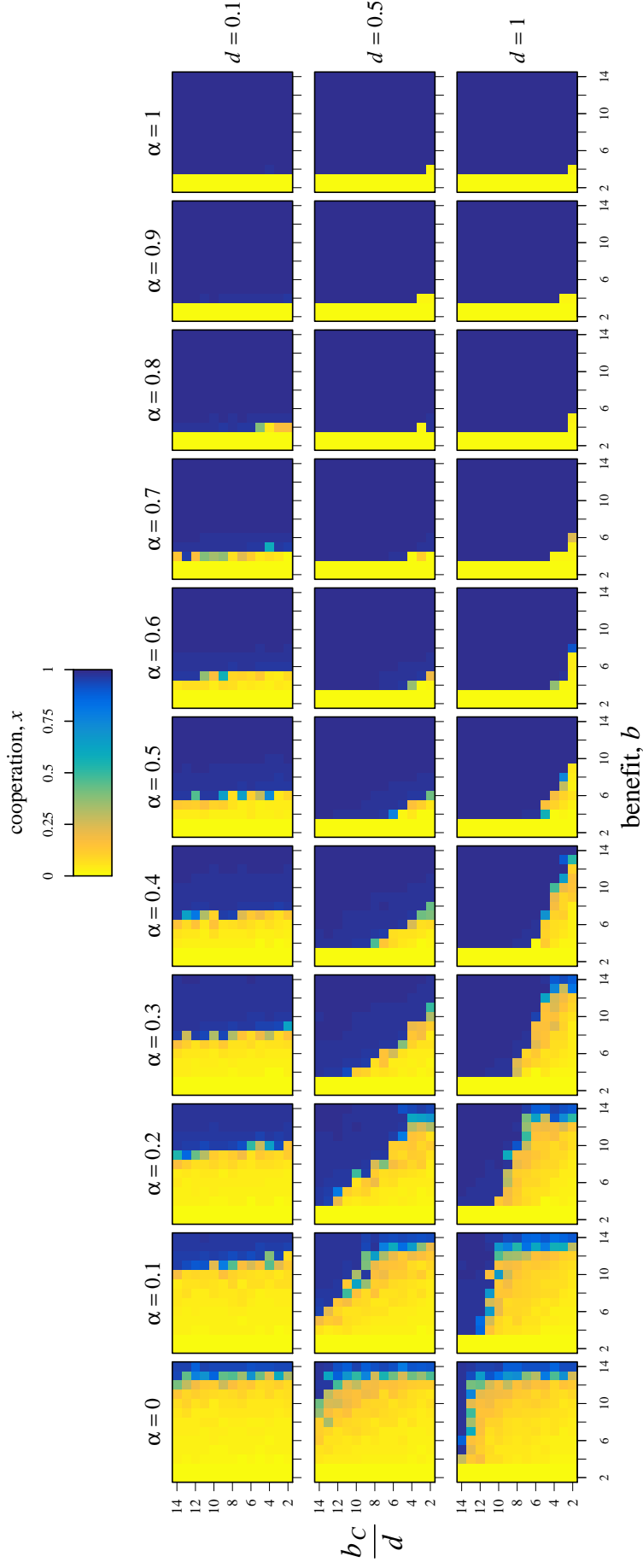
Figure S8: Cooperation strategy x at the end of simulation runs with cognition and $k = 5$. Simulations were started with relatedness $R_o = 0.2$ ($k = 5$) for different values of benefit b, cognition benefit to cost ratio b_C/d and synergy factor α. Half-way through, relatedness was decreased to $R_o = 0.01$ (i.e., $k = 100$). Parameters: $n = 15$, $c = 1$, $\mu = 0.01$, $\sigma = 0.01$.
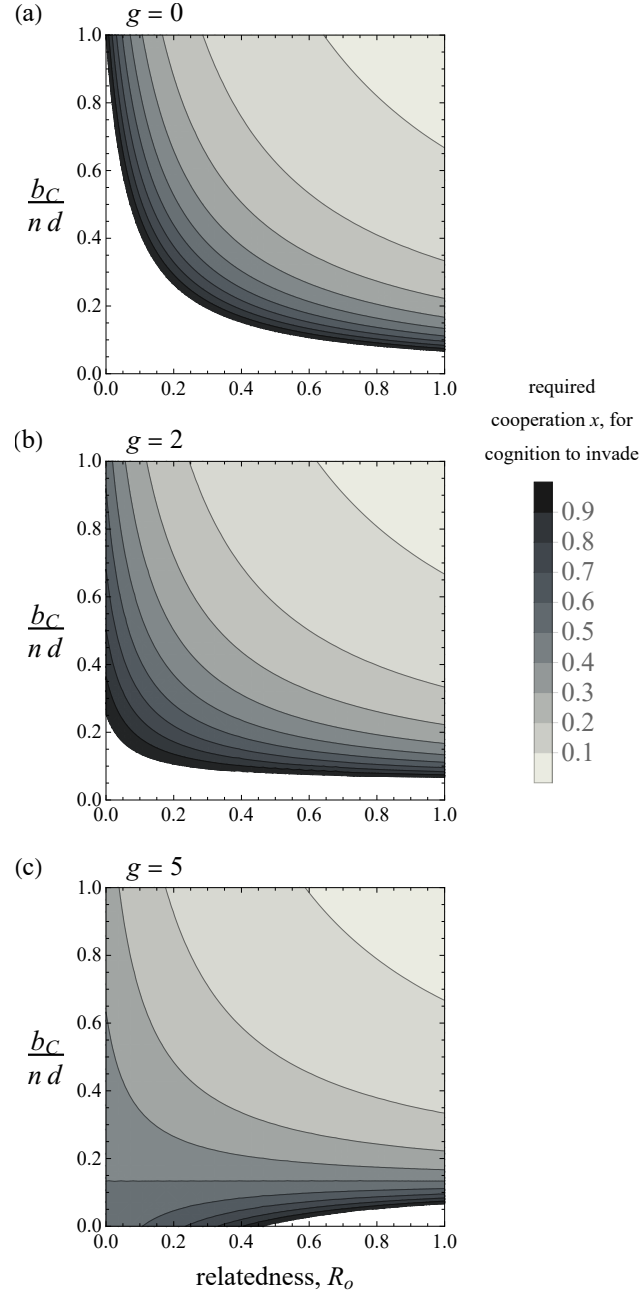
Figure S9: Invasion conditions for Machiavellian cognition. Parameter space where cognition can invade from rarity ($K(x, 0) > 0$), as a function of group size and the per capita share to cost ratio from cognition b_C (scaled by group size n). The parameter g controls the level of exploitation of Machiavellian cognition. Parameters: $n = 15$, $d = 0.5$, $b = 0.2$.

References

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