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Title: The evolution of altruism through war is highly sensitive to population structure and to civilian and fighter mortality

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Abstract

The importance of warfare in the evolution of human social behavior remains highly debated. One hypothesis is that intense warfare between groups favored altruism within groups, a hypothesis given some support by computational modelling and, in particular, the work of Choi and Bowles [Choi J-K, Bowles S. (2007) *Science* 318:636–40]. The results of computational models are, however, sensitive to chosen parameter values and a deeper assessment of the plausibility of the parochial altruism hypothesis requires exploring this model in more detail. Here, I use a recently developed method to reexamine Choi and Bowles' model under a much broader range of conditions to those used in the original paper. Although the evolution of altruism is robust to perturbations in most of the default parameters, it is highly sensitive to group size and migration and to the lethality of war. The results show that the degree of genetic differentiation between groups (F_{ST}) produced by Choi and Bowles' original model is much greater than empirical estimates of F_{ST} between hunter-gatherer groups. When F_{ST} in the model is close to empirically observed values, altruism does not evolve. These results cast doubt on the importance of war in the evolution of human sociality.

Keywords: altruism, war, population structure, parochial altruism hypothesis, fitting to idealized outcomes, agent-based modelling

Significance statement

Many evolutionary theorists have suggested that the human capacity for altruism was forged in war, with cohesive and altruistic groups outcompeting their selfish neighbors. Assessing this 'parochial altruism' hypothesis relies largely on computational modelling. Here, I reexamine a well-known model that explores the co-evolution of altruism and war. As well as clarifying the importance of factors such as the lethality of war to fighters and civilians, the results show that the evolution of altruism in this model relies on a degree of genetic differentiation between groups that exceeds that seen among hunter-gatherers. Furthermore, when the model produces a more realistic population structure, altruism does not evolve, casting doubt on the plausibility of the parochial altruism hypothesis.

Main Text

While humans are capable of cooperation, tolerance, and generosity toward others, we are also capable of prejudice, violence and war. Although superficially at odds, these two sides of human behavior are sometimes closely related, with warfare promoting within-group solidarity and acts of individual sacrifice. The association between intergroup conflict and intragroup altruism has led evolutionary theorists including Darwin [1] to hypothesize that the two may have co-evolved [2–5]. The 'parochial altruism' hypothesis as typically conceived [6] holds that if groups containing more altruistic individuals were able to out-compete groups containing fewer altruistic individuals, this could have provided positive selection for both within-group altruism and out-group hostility ('parochialism') [3,6–8].

The plausibility of the parochial altruism hypothesis depends partly on the likelihood that warfare was commonplace during human evolutionary history, a claim lent some support by archaeological evidence of mass killings [9,10] and ethnographic data from contemporary or historic small-scale societies [11–16] but which remains highly debated [17–20]. However, even if warfare was commonplace in human evolutionary history, this would not necessarily mean that it was an important force in selecting for within-group altruism. Since direct evidence of past selection pressures on altruism and war are unavailable to us, we rely on exploring the co-evolutionary dynamics of parochial and altruistic behaviors using mathematical or computational modelling. Several models exploring parochial altruism have been advanced [2–4,13,21], as part of a wider literature on the possible impact of warfare on the evolution of human sociality [22–25]. Of these models of parochial altruism, arguably the most influential is a model by Choi and Bowles [3]. Choi and Bowles' model suggests that warfare between groups could, in theory, select for both parochialism (out-group hostility) and within-group altruism when individuals form small and genetically differentiated groups that occasionally go to war with one another and where success in these wars is determined by the proportion of parochial altruists in each group.

As set out in other work by Bowles [2,13], differences in the frequency of altruists between groups is critical to the co-evolution of altruism and war - if individuals frequently migrate between groups or if groups are large, altruistic individuals are unlikely to become sufficiently concentrated. This raises the question of how much population structuring is necessary for altruism to evolve in Choi and Bowles' model and how this compares to empirical estimates of population structuring in contemporary small-scale societies. Although previous work on parochial altruism estimated that F_{ST} (a measure of genetic variation explained by differences between groups) was ~0.08 between contemporary hunter-gatherer populations [2], these estimates were based on a wide variety of genetic markers including some which are poor indicators of whole-genome genetic differentiation [26]. Subsequent estimates based on differences in autosomal data suggest that differences between groups who could plausibly compete suggest that it is much lower than this [27–29] and similar to that seen in chimpanzees [26]. This raises two questions for the Choi and Bowles model. First, is the degree of population structure produced by the model similar to empirical estimates? Second, does altruism in the model evolve when population structure is similar to the empirical estimates? As set out by Rusch [6], answering these questions is critical to our assessment of the plausibility of the parochial altruism hypothesis for the evolution of human altruism.

Another reason to explore the Choi and Bowles model in more detail is that while computational modelling can be highly informative, the results of all models will be sensitive to the choice of initial conditions and default parameters. While some parameters can be grounded in ethnographic data, others will be too abstract to ground empirically and in all cases it is important to explore the impact that each parameter has on model outcomes (in this case the evolution of altruism). Most computational models do this by using a fix-all-but-one approach in which one parameter is varied while all others are kept at their default values. Choi and Bowles use this fix-all-but-one sensitivity analysis for five of their model parameters. However, the fix-all-but-one method reduces the exploration of the model outcomes to a small part of parameter space and limits our understanding of the relationship between each parameter and the model outcome and of interactions between parameters [30]. Although the fix-all-but-one approach employed by Choi and Bowles was the standard approach used at the time, methods have subsequently been developed to explore model parameter space more fully [30–32]. Here, I use a Fitting to Idealized Outcomes method developed by Gallagher, Shennan, and Thomas [30] to reexamine the results of Choi and Bowles' model of parochial altruism in order to (*i*) explore the results of the model in more detail and under a broader range of conditions, and (*ii*) calculate the degree of population structure produced by the model and compare this to empirical estimates. I find that while warfare in the model can lead to the evolution of altruism, it only does so when groups are far more genetically differentiated than groups of contemporary hunter-gatherers are estimated to be.

Choi and Bowles model

In their model [3], Choi and Bowles consider a population living in 20 groups of n agents. Agents have a behavioral phenotype determined by two 'genes'. The first determines whether they are 'altruistic' (A) or 'nonaltruistic' (N) and the second determines whether they are 'tolerant' (T) or 'parochial' (P). Thus, an agent can be a parochial altruist (PA), parochial non-altruist (PN), tolerant altruist (TA), or tolerant non-altruist (TN). In each generation of the model, there is a within-group interaction and a between-group interaction. The within-group interaction consists of a 'public goods' game in which altruists pay a cost (c) to contribute a benefit (b) to a communal pot that is then divided equally between all group members. All else being equal, the dominant strategy in this game is to be a non-altruist 'free-rider' who receives benefits from altruistic group mates without paying a cost themselves. However, the model also contains a between-group phase in which groups are randomly paired with another group and have an interaction that can be either hostile or tolerant. The probability of the interaction being tolerant is determined by the proportion of tolerant agents in the two groups. If a tolerant interaction occurs, tolerant agents receive a positive fitness payoff equal to the number of tolerant agents in the rival group multiplied by the parameter g. If a hostile interaction occurs, the groups will go to war with a probability determined by the difference in the proportion of parochial agents in each group. Thus, while all parochial agents (PAs and PNs) can be thought of as agitating for hostility, only parochial altruists (PAs) actually 'go to war' as fighters. War can result in either a draw or with the group with more parochial altruists winning. When a draw occurs, fighters die with a probability determined by the parameter δ_f and are replaced by the offspring of surviving members of their own group. When the group with more parochial altruists wins, fighters on both sides die with the probability δ_f and civilians (i.e. non-PAs) of the losing group die with a probability determined in part by the parameter δ_c and all dead agents are replaced by the offspring of surviving members of the winning group. When reproduction occurs, new agents mutate to a random phenotype with probability μ. Each generation, a proportion of agents from each group determined by parameter m migrate to a random group (although note that since agents may replace dead members of other groups during war, this migration is not the only way for genes to move between groups). In addition to the original model, I added a third 'gene' with six alleles that is inherited and mutates with the same probability as the 'altruism' and 'parochialism' genes but which has no effect on fitness. This 'neutral' gene allows the measurement of population structure from locus that is not under selection [33].

Results

I replicated Choi and Bowles' original model and carried out 60,000 simulations. In each simulation parameters were set randomly within the ranges listed in Table 1 and model outcomes were recorded. Across these simulations, the mean proportion of altruists in the population (f^A) was strongly correlated with group size and migration rate, moderately associated with the lethality of war to both fighters and civilians and with the costs of altruism in the public goods game, and weakly associated with the payoffs of tolerance toward neighboring groups (Table 2). Of the 60,000 simulations, 29,158 (48.6%) resulted in a mean proportion of altruists in the population across all generations (f^A) of > 0.5. Histograms of the parameters that produced these 29,158 simulations are shown in Figure 1.

Altruism and the lethality of war

Two parameters determine the lethality of warfare in the model: δ_f and δ_c. For the proportion of fighters dying in war (δ_f), there is a moderate negative relationship with the proportion of altruists (ρ = -0.17) such that altruism is more likely to evolve ($f^A > 0.5$) when fewer fighters die in war (Fig 1a). Conversely, for the parameter that determines the probability of civilians dying (δ_c), there is a strong positive relationship with the proportion of altruists (ρ = 0.32) such that altruism is unlikely to evolve unless civilians (who are all non-PAs) die in war. These parameter-expanded results demonstrate two intuitive but important points – that parochial altruism will not evolve unless a large proportion of fighters (and their PA phenotypes) survive, and a moderate or large proportion of civilians (and their non-PA phenotypes) die when the fighters from their group lose in war. These results lend support to a central feature of the Choi and Bowles model - that altruism in the model is selected as a result of the dynamics of warfare between groups. Fix-all-but-two simulations varying δ_f and δ_c show that increases in δ_c and decreases in δ_f from the default values make it unlikely that $f^A > 0.5$ (Fig 2a).

Intragroup altruism and intergroup tolerance

During the within-group phase of the model altruists pay a fitness cost (*c*) which was negatively correlated with f_A across simulations (ρ = -0.33) such that altruism was less likely to evolve when being an altruist had a higher fitness cost (Fig 1c). Fix-all-but-two simulations show that the benefit that altruists provide to group mates has virtually no effect on the evolution of altruism (Fig 2b). Similarly, the payoffs of tolerant interactions with other groups (parameter *g*) are only weakly associated with f_A across the parameter range explored here (ρ = -0.05, Fig 1d).

Population structure

The two parameters that were most strongly correlated with f_A were group size (*n*) and migration between groups (*m*). There were strong negative correlations between these parameters and f_A such that altruism was less likely to evolve when groups were larger and migration between groups was more frequent (Table 2, Fig1e-f). The sensitivity of the model results to *n* and *m* can be clearly seen in the fix-all-but-two simulations shown Fig 2c – modest increases in these parameters from the default values of $n = 26$ and m = 0.25 would mean that f_A is unlikely to exceed 0.5. These parameters are so influential because they determine the degree of genetic differentiation between groups in the model, as shown by the strong negative correlations between F_{ST} and *n* ($\rho = -0.95$) and *m* ($\rho = -0.16$) and between F_{ST} and f_A ($\rho = 0.65$, Table 2).

Ethnographic comparison

Given the importance of group size (*n*) and migration (*m*) to the evolution of altruism in the model, it is important to select these values carefully; establishing parameters that reflect a plausible scenario in human evolutionary history is critical to our interpretation of the model and the plausibility of the parochial altruism hypothesis for humans. To do this it is necessary to establish the degree of population structure produced in the model and compare this with ethnographic estimates of $F_{ST.}$

Mean F_{ST} under Choi and Bowles' default parameters is 0.083 (SD = 0.008, averaging over 100 simulations of 50,000 generations). This is ~3 times greater than the estimates of mean pairwise F_{ST} of 0.012 (SD = 0.016) between hunter-gatherer groups (Fig 3a, Table S1) and those reported for chimpanzees of 0.014 (SD = 0.009) [26]. None of the simulations explored above produced $F_{ST} < 0.02$, so an additional set of simulations were run across even more expanded parameter ranges for *n* and *m* ($0 \leq m \leq 1$ and $6 \leq n \leq 200$) to identify parameter sets that would produce F_{ST} close to the empirical estimates. Values close to the mean empirical F_{ST} estimate (0.012 +/- 0.005) are produced when groups are much larger (mean $n = 96.6$) and migration is much more frequent (mean $m = 0.51$) than the default values of $n = 26$ and $m = 0.25$. In simulations that produced F_{ST} close to this ethnographic estimate, the proportion of altruists and parochial altruists evolving in the model was much less than that observed in the default values from the original model (Fig 3b-c). In short, the degree of genetic differentiation between groups produced by Choi and Bowles' original model is far greater than that seen between hunter-gatherer populations (Fig 3a) and when F_{ST} in the model is close to these ethnographically observed values, altruism does not evolve (Fig 3b-c).

Discussion

Here, I have reexamined Choi and Bowles' model of parochial altruism, using a Fitting to Idealized Outcomes (FIO) method to explore parameter space more fully and estimating the degree of population structure produced. The results of this reanalysis support the general claim that intense competition between groups could, in theory, favor within-group altruism but suggest that this is only likely to occur when groups are far more genetically differentiated from each other than contemporary hunter-gatherer groups are estimated to be [26]. Under parameter regimes that produce a population structure similar to those that have been empirically observed, parochial altruism does not evolve in the model.

The importance of population structure to the outcome of the model is consistent with work by Bowles on population structure and social evolution [2,13] and with the importance of population structure for explanations for social evolution more generally [34–37]. Indeed, at a certain degree of abstraction all explanations for the evolution of altruism rely on population structuring of some kind [34,37–39]. For humans, the low degree of genetic differentiation seen between hunter-gatherer groups [26] is likely to be a consequence both of specific features of hunter-gatherer social organization such as bilocal residence [40] and high mobility [41] and also of more general features of human social organization such as tolerant relationships with neighbors facilitated by the recognition of affinal kinship (i.e. relationships with in-laws) [42,43], and the formation of multi-level societies [44,45]. Although these features of social organization were not necessarily present throughout the entirety of human evolutionary history, there are also general features of ape life-history that are likely to reduce genetic differentiation between groups by reducing intragroup relatedness. These include the production of single offspring rather than litters, multiple juvenile cohorts, and low female reproductive skew [46,47] and may explain why estimates of F_{ST} are similar in chimpanzees and humans despite differences in social organization [26,48,49]. Taken together, human life-history and social organization are unlikely to produce degrees of genetic differentiation between groups that are sufficient for intergroup conflict to favor intragroup altruism in the Choi and Bowles model.

It is important to emphasize that the results of this analysis make no comment on the frequency of war in human evolutionary history and do not dispute that the co-evolution of altruism and intergroup conflict is a theoretical possibility more broadly. In fact, this reanalysis clarifies the factors that may promote the evolution of altruism through intergroup conflict. Specifically, the evolution of altruism in the model is promoted by low fighter mortality (low δ_f) and high civilian mortality during war (high δ_c), a small cost to altruism in within-group interactions (low *c*), small payoffs to tolerant interactions with neighbors (low *g*), and by small groups with low rates of migration between them (small *n* and *m*). Even if these conditions were not met in humans, they may be met in other group-living mammals living in small but genetically differentiated groups among which intergroup aggression is frequent such as meerkats [36,50], wolves [52], and banded mongooses [51]. For banded mongooses, the observed degree of genetic differentiation between groups (F_{ST} = 0.129) [51] would be sufficient for altruism to evolve in the Choi and Bowles model. It is worth noting that the Choi and Bowles model assumes that all parochial altruists will go to war whereas in actual human societies active participation in war is usually restricted to young men [12,22]. Negative fitness consequences of parochial altruism in non-combatants would mean that altruism is less likely to evolve and may lead to intrafamilial and intergenerational conflicts of interest, especially if the spoils of war are unequally distributed [22,23].

The findings from this analysis provide further demonstration of the utility of the Fitting to Idealized Outcomes method [30] for fully exploring the results of computational models. They highlight the conditions necessary for the evolution of altruism through war and suggest that altruism will only evolve in Choi and Bowles' model of parochial altruism when competing groups are far more genetically differentiated than they are likely to have been in human evolutionary history.

Methods

I translated the Choi and Bowles model [3] into R using a combination of the published description of the model and their original MATLAB code and successfully replicated the main results of their paper and the original sensitivity analysis (Figs S1-2). To fully explore the results of the model across parameter space, I used the 'Fitting to Idealized Outcomes' method set out by Gallagher et al. [30] (also see [31,46]). I ran the model 60,000 times and in each simulation randomly set parameters within defined limits within which the default parameter from Choi and Bowles was the mean (Table 1). In each case, I recorded frequencies of the four phenotypes across 10,000 generations. This was sufficient to provide stable estimates of relationships between parameters and model outcomes (Fig S3). Two parameters from the initial model were treated as constants: mutation rate (μ) was kept at the default value of 0.005 in all simulations as there was little theoretical justification for varying it and the number of groups in the population was kept at 20 as initial simulations suggested it had no effect on model outcomes. In the main simulations the cost of contributing to the within-group public good (c) was varied but the benefit (b) was not; initial simulations suggested that b had little effect on the model outcome (as demonstrated in Fig 2b). In addition to the 50,000 simulations, I explored three pairs of parameters (n and m, δ_c and δ_f, c and b) under even broader parameter ranges, randomly setting the two parameters of interest 2,500 times but fixing all other parameters to the default values from the original simulation (a 'fix-all-but-two' approach). I also ran 2,000 additional simulations with larger upper bounds for group size and migration ($0 \leq m \leq 1$ and $6 \leq n \leq 200$) to find F_{ST} values close to empirical estimates (0.012 +/- 0.005). In these simulations all other parameters were set to default values.

Comparing empirical and simulated genetic differentiation

In order to compare the degree of genetic differentiation produced in Choi and Bowles' model with empirical estimates I calculated F_{ST} for a neutral six-allele 'gene' which is inherited and mutated in the same way as the altruism or parochialism genes but which is unlinked to them and which does not influence fitness and is therefore considered a 'neutral' locus. Six alleles approximates the mean 6.4 alleles for the microsatellite data included in Verdu et al. discussed below [27]. As defined by Nei [53], F_{ST} (sometimes known as G_{ST} for polyallelic loci) is calculated as $(H_T - H_S)/H_T$ where H_S is the average Hardy-Weinberg heterozygosity across groups and H_T is the total population heterozygosity. Although (as pointed out by Hedrick [54]) F_{ST} estimates will potentially vary with allele number, F_{ST} for the neutral locus in this model is robust across allele number (Fig S4). As an additional check, I also compared empirical and simulated genetic differentiation according to the standardized measure G'_{ST} as defined by Hedrick [54]. Doing so produced very similar results (Fig S5).

Empirical estimates of pairwise genetic differentiation between populations of contemporary hunter-gatherers are listed in Table S1 and were based on microsatellite data from Australian [29], South American [28], and Central African [27] populations compiled by Langergraber et al. [26] with some exclusions. The data exclusions are of the pairwise differences between the Australian populations not listed as being from the more remote Arnhem, Gulf, or North regions listed in Walsh et al. [29]. The excluded populations are those in which it is likely that there have been higher rates of recent migration and admixture. Since the mean F_{ST} in the remote groups was higher than that among the Australian groups in general, excluding the non-remote data increases the empirical estimates of genetic differentiation. The remaining data set consists of 30 pairwise comparisons between contemporary hunter-gatherer populations, with a mean geographic distance between pairs of 270km (Table S1). To reduce computing time, F_{ST} was calculated in a subset of 10,000 of the 60,000 simulations.

Data Availability. Model code is available in the supporting information.

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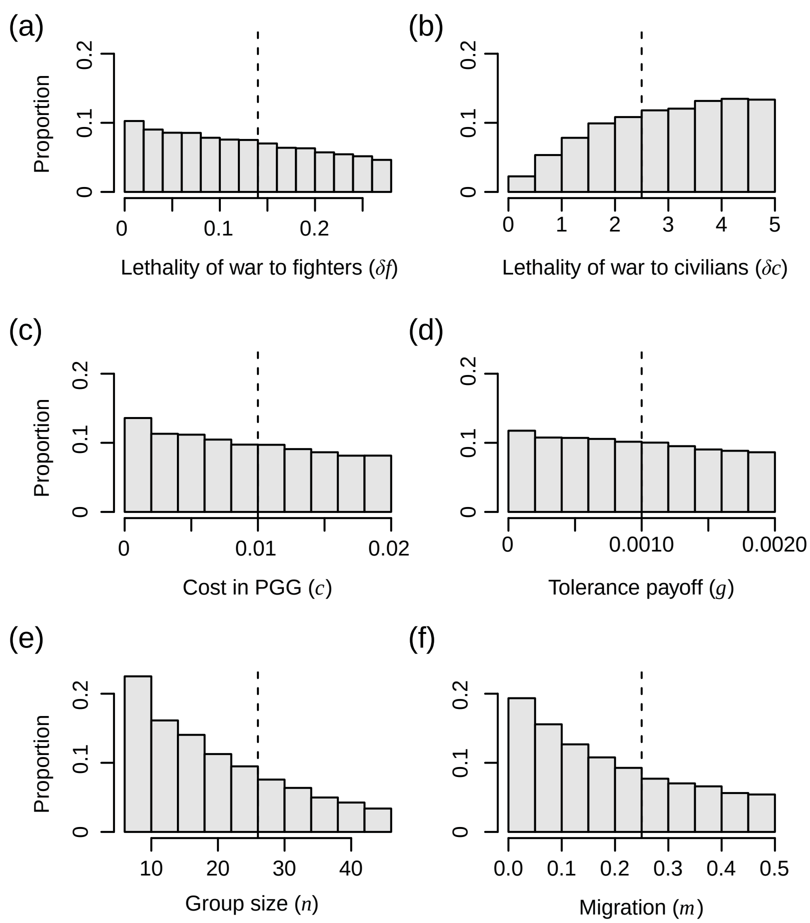
Figure 1: Conditions favoring the evolution of altruism. Histograms showing the parameter values from the 29,158 simulations in which mean f^A across generations exceeded 0.5. Dotted lines indicate the default parameter values from the Choi and Bowles model.

Figure 2: Parameter interactions in 'fix-all-but-two' simulations. Evolution of altruism when varying pairs of parameters relating to (a) warfare, (b) the payoffs of within-group cooperation, and (c) population structure. In each panel, dots represent simulations in which $f_A > 0.5$. The red triangle represents the parameter values from the original model.

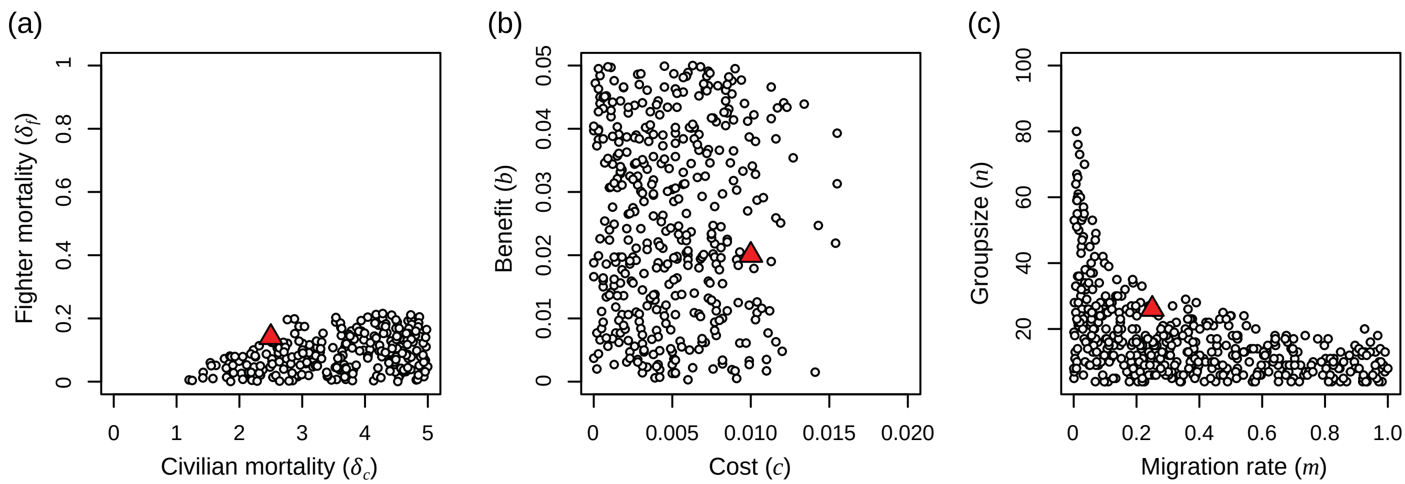
Figure 3: The effect of population structure on model outcomes. (**a**) logistic regression predicting the probability of altruism evolving in a simulation (mean f_A across generations > 0.5) and F_{ST} across 2,000 simulations in which n and m were varied ($0 \leq m \leq 1$ and $20 \leq n \leq 200$) and all other parameters were kept at default values, (**b**) mean proportion of altruists in the model (f_A) under parameter sets that produce F_{ST} values close to (within +/- 0.005) those empirically observed and under the Choi and Bowles default values, (**c**) mean proportion of parochial altruists (f_{PA}) in the model under parameter sets that produce F_{ST} values close to (within +/- 0.005) those empirically observed and under the Choi and Bowles default values

Table 1: Parameters, constants, and outcomes of the model.

Table 2: Spearman's correlation coefficients between each parameter or outcome and the proportion of altruists (f^A), parochials (f^P), parochial altruists (f^{PA}), and F_{ST} in the population averaged across 60,000 simulations (F_{ST} values from 10,000 simulations only).



(a)
Proportion
Lethality of war to fighters (δf)
(b)
Lethality of war to civilians (δc)
(c)
Proportion
Cost in PGG (c)
(d)
Tolerance payoff (g)
(e)
Proportion
Group size (n)
(f)
Migration (m)


(a)
Fighter mortality (δ_f)
0
0.2
0.4
0.6
0.8
1
0
1
2
3
4
5
Civilian mortality (δ_c)
(b)
Benefit (b)
0
0.01
0.02
0.03
0.04
0.05
0
0.005
0.010
0.015
0.020
Cost (c)
(c)
Groupsize (n)
20
40
60
80
100
0
0.2
0.4
0.6
0.8
1.0
Migration rate (m)

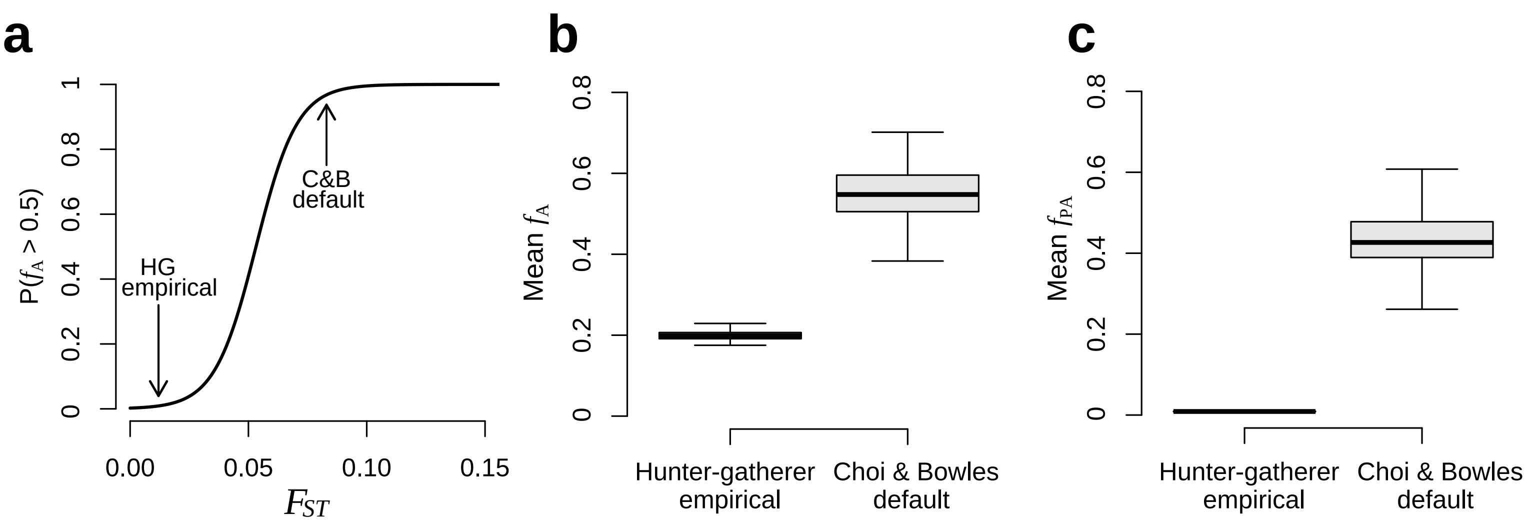

a
b
c
P(f_A > 0.5)
1
0.8
0.6
0.4
0.2
0
HG
empirical
C&B
default
0.00
0.05
0.10
0.15
F_{ST}
Mean f_A
Mean f_{PA}
Hunter-gatherer
empirical
Choi & Bowles
default

Table 1: Parameters, constants, and outcomes of the model.

Type	**Symbol**	**Description**	**Default value**	**Range or value used in FIO simulations**
Parameter	n	Group size	26	[6,46]
Parameter	g	Tolerance benefit	0.001	[0,0.002]
Parameter	δ_c	Lethality of war to civilians	2.5	[0,5]
Parameter	δf	Lethality of war to fighters	0.14	[0,0.28]
Parameter	m	Migration	0.25	[0,0.5]
Parameter	c	Public goods game cost	0.01	[0,0.02]
Constant	μ	Mutation rate	0.005	0.005
Constant	-	Number of groups	20	20
Constant	b	Public goods game benefit	0.02	0.02
Outcome	f^A	Mean proportion of altruists over all generations	-	-
Outcome	f^P	Mean proportion of parochialists over all generations	-	-
Outcome	f^{PA}	Mean proportion of parochial altruists over all generations	-	-
Outcome	F_{ST}	Genetic differentiation between groups	-	-

Table 2: Spearman's correlation coefficients between each parameter or outcome and the proportion of altruists (f^A), parochials (f^P), parochial altruists (f^{PA}), and F_{ST} in the population averaged across 60,000 simulations (F_{ST} values from 10,000 simulations only).

Symbol	Parameter/outcome	f^A	f^P	f^{PA}	F_{ST}
n	Group size	-0.54	-0.64	-0.63	-0.95
m	Migration	-0.45	-0.42	-0.43	-0.16
c	Public goods game cost	-0.33	-0.05	-0.16	0.00
δ_c	Lethality of war to civilians	0.32	0.28	0.30	0.04
δ_f	Lethality of war to fighters	-0.17	-0.15	-0.16	0.04
g	Tolerance benefit	-0.05	-0.28	-0.23	-0.01
F_{ST}	Genetic differentiation of groups	0.65	0.76	0.74	-