

Acculturation drives the evolution of intergroup conflict

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Conflict between groups of individuals is a prevalent feature in human societies. A common theoretical explanation for intergroup conflict is that it provides benefits to individuals within groups in the form of reproduction-enhancing resources, such as food, territory, or mates. However, it is not always the case that conflict results from resource scarcity. Here, we show that intergroup conflict can evolve, despite not providing any benefits to individuals or their groups. The mechanism underlying this process is acculturation: the adoption, through coercion or imitation, of the victor's cultural traits. Acculturation acts as a cultural driver (in analogy to meiotic drivers) favoring the transmission of conflict, despite a potential cost to both the host group as a whole and to individuals in that group. We illustrate this process with a two-level model incorporating state-dependent event rates and evolving traits for both individuals and groups. Individuals can become "warriors" who specialize in intergroup conflicts, but are costly otherwise. Additionally, groups are characterized by cultural traits, such as their tendency to engage in conflict with other groups and their tendency for acculturation. We show that, if groups engage in conflicts, group selection will favor the production of warriors. Then, we show that group engagement can evolve if it is associated with acculturation. Finally, we study the coevolution of engagement and acculturation. Our model shows that horizontal transmission of culture between interacting groups can act as a cultural driver and lead to the maintenance of costly behaviors by both individuals and groups.

group selection | cultural evolution | intergroup conflict

Intergroup hostility, ranging from intermittent skirmishes to large-scale conflicts, is a recurrent event in human history (1, 2). It has been suggested that it contributed to shaping our species' social behaviors (3) and that it played a role in our organization in complex societies (4). Although intergroup conflict was not universal among nonstate societies (5, 6), it was nonetheless frequent enough that 64% of hunter-gatherer groups engaged in violent conflict at least once every 2 y (6). Intergroup conflict was not just frequent, but also costly, causing an estimated 14% of total mortality in hunter-gatherer societies (3) (but see also ref. 7).

Evolutionary anthropologists have used a variety of approaches and methods to understand the prevalence of intergroup conflict in the face of such costs (reviewed in ref. 8). For example, behavioral ecologists highlight the importance of reproductive benefits that can be acquired by members of successful groups (9). If the benefits of fighting are sufficiently large, if the costs are sufficiently low, or if the belligerent party has little to lose (i.e., the "value of the future" is low), then we should expect intergroup conflict (10). The costs of initiating conflict could be low if group dynamics leads to vastly different group sizes, providing relative safety to large groups (11). Evolutionary psychologists, in turn, focus on the psychological mechanisms that underlie coalitional violence, based on the assumption that such mechanisms were shaped by natural selection. For example, the "risk contract" theory suggests

that individuals will be willing to engage in war if success is likely and if participants are rewarded (12), whereas the "male warrior hypothesis" argues that men have psychological traits that allow them to use intergroup conflict to protect or acquire reproductive resources (13). Anthropologists have noted that, apart from collective benefits such as territory, there are also private incentives to participating in group conflict (14–16). In addition, groups can also sanction free-riders (17). Common to most of these approaches is the idea that the costs of conflicts are ultimately outweighed by individual or collective benefits, often in the form of resources [including food, territory, or mates (15, 18, 19)]. Because of their emphasis on reproduction-enhancing resources, many authors within these traditions (e.g., refs. 9, 11, 19, and 20) propose an evolutionary link between human intergroup conflict and the coalitional aggression behaviors that are prevalent among other animals, such as ants, termites, and chimpanzees.

One prediction of this framework is that resource scarcity should be positively associated with the frequency and/or magnitude of intergroup conflicts (21). However, the empirical evidence for this association is mixed. For example, whereas land shortages (22) and natural disasters (23) seem to predict warfare, chronic resource scarcity and a lack of potential mates do not (23). Overall, literature reviews (21, 24) suggest that there is no robust quantitative link between resource scarcity and intergroup conflict.

Significance

We propose a mechanism for the cultural evolution of conflicts between groups of individuals. The traditional explanation for the persistence of these conflicts is that they provide benefits for winners, such as resources owned by other groups. We offer an alternative explanation, which does not rely on resource acquisition. We argue that acculturation—the adoption of the victor's culture following defeat—can promote the evolution of conflicts, even though they are detrimental for all individuals. We call this mechanism "cultural drive," in analogy to meiotic drive, where deleterious alleles spread by increasing their own rate of transmission. Our study suggests that multilevel selection can have important and unexpected consequences for cultural evolution, highlighting the usefulness of this framework.

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Data deposition: Simulation code and data have been deposited in GitHub, <https://github.com/GilHenriques/acculturation2019/tree/master>.

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This raises the possibility that, in addition to resource-associated benefits, there may be alternative explanations for intergroup conflict. How can we explain the prevalence of this costly behavior in cases where it does not provide benefits to the winners? In genetic evolution, some alleles spread, despite being detrimental to carriers by increasing their own rate of transmission, in a process called meiotic drive (25). Drivers underlie such costly phenomena as reduced sperm count in males (26) and spore killing in fungi (27). In cultural evolution, a similar process of biased transmission between individuals has been invoked to explain the spread of costly behaviors such as food taboos or religious rituals (28). An analogous process of transmission of cultural traits between groups (acculturation) could act as a driver for the evolution of costly group behaviors such as intergroup conflict in human societies.

An example of acculturation is the adoption (either by coercion or imitation) of the victor's cultural traits following military defeats. For example, following the expansion of the Roman empire, native European tribes adopted elements of Roman culture, such as language, eating habits (29), religion (30), and laws (31). They also adopted Roman military techniques and weapons, occasionally using them against the Romans themselves (32). Modeling suggests that conflict-associated acculturation could be responsible for the spread of social traits and military technology (4), but could it also explain the tendency of groups to engage in costly conflicts?

In this work, we will give a proof of principle that intergroup conflict can be explained, even in the absence of direct or indirect material benefits to either individuals or groups. In particular, we argue that acculturation can drive the evolution of costly antagonistic behaviors such as engagement (i.e., the tendency to initiate conflicts). Because we are dealing with human cultural traits and their effects on population dynamics, we will use cultural evolutionary theory (33, 34), in which individuals are characterized by cultural traits. These traits can be transmitted between individuals and change over time by a process reminiscent of natural selection. Furthermore, like refs. 35 and 36, we consider that group dynamics cannot be fully described solely by considering individual traits. Instead, we also consider group-level traits [sometimes called social institutions (35) or ultrasocial norms (4, 37)]. Such group-level traits represent the phenotypic effects of generalized conventions or organized structures which may differ among groups and which are not reducible to individual behaviors, such as professionalized government, monogamous or polygamous mating systems, resource inheritance, etc. (36). Much like individuals are bearers of genetic or cultural traits, groups are bearers of institutions (35). In our model, being a warrior is a property of individuals, but engagement and acculturation tendency are properties of groups.

To simultaneously study the dynamics of individuals and groups, we use the framework of group (multilevel) selection (38). In this framework, the population and evolutionary dynamics are determined by state-dependent event rates for both individuals and groups, resulting in a two-level population process (38). Individual-level events are births and deaths of individuals that occur within a given group and affect the composition of that group—i.e., the number of individuals and their cultural traits. Group-level events affect whole groups and consist of group fissions, group extinctions, and interactions (conflicts). Following ref. 38, a trait evolves by (cultural) group selection if its evolution requires group-level events. The evolution of human culture by group selection is called cultural group selection, particularly in the context of intergroup conflict (39–41).

Model Description

Consider a population consisting of a number of distinct groups of individuals. For simplicity, these individuals are assumed to

be haploid and asexually reproducing. The size and composition of groups vary over time due to the birth and death of individuals (within-group dynamics). Similarly, the number of groups changes due to group-level events—namely, fissions, extinctions, and intergroup conflicts (between-group dynamics).

Within-Group Dynamics. Individuals belong to one of two classes—warriors or shepherds—whose within-group densities are denoted by real variables x and y , respectively. Individuals are characterized by a cultural trait $p \in [0, 1]$, which is the probability that their offspring becomes a warrior (so that $1 - p$ is the probability that an offspring is a shepherd). This trait is inherited vertically from one's parent, with some probability of mutation. Later, we will allow for horizontal transmission of this trait through the process of acculturation. Although we refer to the two classes as “shepherds” and “warriors,” these names are just evocative labels and do not need to refer to their literal meaning. More abstractly, we could refer to warriors as “intergroup conflict specialists.”

To ensure density regulation within groups, the birth rate of shepherds decreases exponentially with group density:

$$b(x, y) = b_1 + b_2 e^{-(x+y)b_3}, \quad [1]$$

where the parameters b_1 , b_2 , and b_3 can be interpreted, respectively, as minimum birth rate, difference between maximum and minimum birth rate, and sensitivity to density dependence.

We assume that warriors have a lower birth rate than shepherds. This assumption implies that producing warriors represents a cost to shepherd individuals, with higher values of p corresponding to higher costs. In general, the birth rate of warriors is $(1 - c)b(x, y)$, with the parameter $0 \leq c \leq 1$ regulating the cost of warrior production. The worst-case scenario for the evolution of conflict occurs when $c = 1$ (nonreproductive warriors); for this value, producing warriors is a “reproductive sink” for shepherds. For the majority of this work, and unless otherwise stated, we will focus on this most conservative case, but our results also generally apply to cases where $c < 1$.

In general, death rates could also be density- (and class-) dependent, but for simplicity, we consider the case of a constant per capita death rate d for all individuals. Due to the cost of producing nonreproductive warriors, within each group, there is individual-level selection for low values of p . The differential equations governing within-group dynamics are given in Materials and Methods.

Between-Group Dynamics. Group dynamics are governed by three types of events: fissions, group extinctions, and group interactions (conflicts). The rates at which these events occur in a given group depend in general on both the composition of the group and the number and composition of all other groups in the population. They can also depend on the group's cultural traits. Just like individuals are characterized by a cultural trait p , groups are characterized by group-level traits, which may represent cultural institutions, fashions, or conventions. These institutions govern the collective behavior of the group and are not reducible to the properties of the group's constituent individuals. We consider two such cultural traits—engagement (q) and acculturation tendency (r)—which are relevant for conflict initiation and resolution, respectively.

Group Extinctions. When a group extinction occurs, the group is removed from the population. This event reflects the possibility that whole groups of individuals collapse due to, for example, a bad harvest, intragroup strife, or natural catastrophes (but

not due to a hostile interaction with another group, which is a separate event). We assume that the group extinction rate is a decreasing function of the number of individuals within the group and an increasing function of the number of groups (see *SI Appendix* for details). Thus, higher-density groups are less likely to go extinct, and extinctions are more frequent when there are more groups, leading to regulation at the level of groups.

Fissions. When a group fissions, it divides into two autonomous daughter groups, which inherit the group-level traits (q and r) of their parent group, modified by normally distributed mutations with $SD \sigma_q, \sigma_r$. The fission rate is linearly proportional to group density, so that bigger groups are more likely to undergo fission (see *SI Appendix* for details). Because groups that produce many warriors have lower densities (see below), they also have lower fissioning rates. Thus, warrior production is counteracted not just by individual selection, but also by the faster proliferation of groups with fewer warriors.

In the event of a fission, the division of individuals among the daughter groups is assortative with respect to the value of the individual trait p , such that the most extreme individuals are more likely to group together with individuals similar to themselves, whereas the most common individuals are more likely to separate at random. The degree of assortment is regulated by a parameter s (see *SI Appendix* for details). Such assortment, called “associative” splitting by Hamilton (42), is to be expected if splitting occurs over internal political disagreements or if splitting occurs along family lines, both of which are common in human societies (43). Assortment increases variability between groups, enhancing the effect of group selection (42, 44).

Group Interactions. Earlier models of intergroup conflict assumed that individuals expressed a belligerence trait and that groups initiated conflicts with a probability proportional to the average level of this trait within the group (18, 19, 45). In contrast, in our model, the tendency to engage in conflicts is a group-level trait, $q \in [0, 1]$. A given group initiates a conflict at a rate which is proportional to its engagement trait and to the total number of groups N :

$$G(q, N) = \gamma N q. \quad [2]$$

Once a focal group initiates a conflict, a rival group is chosen at random (i.e., there is no spatial structure in the model). The focal group wins the conflict with a probability that depends on

the difference between the numbers of warriors of the opposing factions (for more details, see *SI Appendix*). The resolution of the conflict, in turn, depends on the victor's acculturation tendency $r \in [0, 1]$. With probability $1 - r$, the defeated group is removed from the population (similar to an extinction event); otherwise, it undergoes acculturation—i.e., it adopts the victor's cultural traits (with mutations, as described above). Individuals within the group adopt variants of p in proportion to their frequency in the victorious group. We will also consider the robustness of our results to the possibility of “costly” acculturation, in which a fraction of individuals die during the conflict before acculturation.

Results

Population Dynamics within Groups. In the absence of group events, the equilibrium within-group density of individuals, $\hat{n}(p) = \hat{x}(p) + \hat{y}(p)$, is lower for groups with higher mean p (see *SI Appendix* for details). Thus, groups that produce higher fractions of warriors support fewer individuals, because warriors are nonreproductive (*SI Appendix*, Fig. S1A). Note that in the course of the two-level process, population dynamics within groups does not necessarily have time to reach the equilibrium (described by *SI Appendix*, Eq. S5), especially if the frequency of group events is sufficiently high. Frequent fissioning events, on the one hand, and within-group evolution toward lower values of p , on the other, result in actual within-group densities that are lower than one would predict based on the equilibrium condition above. This is illustrated in Fig. 1A, which compares realized group densities for different values of p with the predicted equilibrium.

Because increased p causes a decrease in the total group density, the maximal density of warriors is attained for an intermediate value of p , such that $\partial_p \hat{y}(p) = 0$. With the reference parameters (*Materials and Methods*), the number of warriors is maximized when $p \approx 0.514$ (*SI Appendix*, Fig. S2A).

Since warriors do not reproduce, p evolves to a mutation-selection balance near zero in the absence of group events, at which point groups consist almost exclusively of shepherds and have maximal density. Thus, in our simulations, any significant production of warriors at equilibrium must result from the effects of group events.

Frequent Intergroup Conflict Promotes Warrior Production. As a starting point, we first consider engagement q to be a constant, rather than an evolving, trait. We also set $r = 0$ (i.e., no

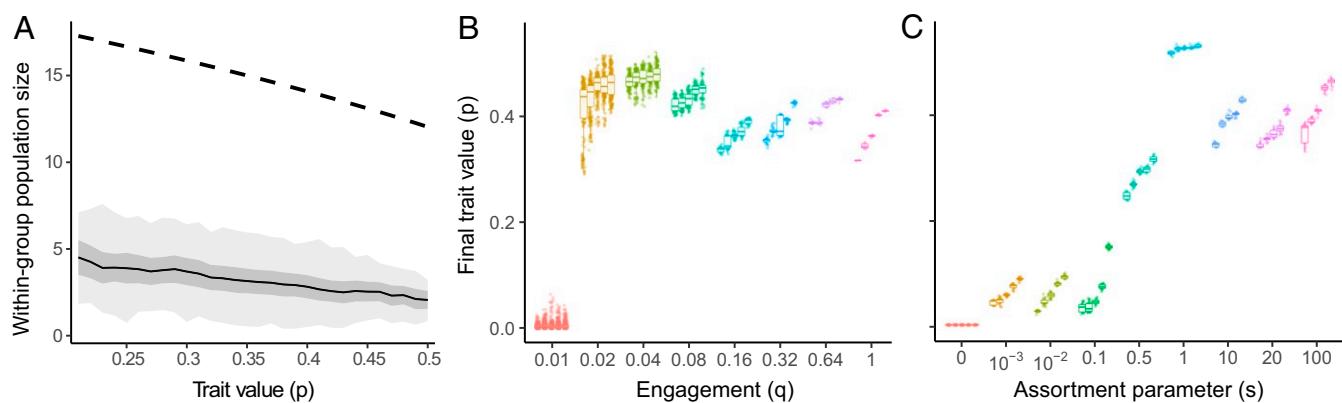


Fig. 1. Evolution of warrior production with constant group-level traits. (A) Increased warrior production leads to smaller groups. Five replicate simulations with constant $q = 0.64, r = 0$ were grouped together to calculate mean group density in groups with different mean p . Dark ribbon shows standard deviations, and light ribbon indicates the full range of values. The dashed line shows estimated equilibrium values (*SI Appendix*, Eq. S5). (B and C) Effect of engagement and assortment on warrior production. Each point indicates a group's mean p after equilibrium has been reached, when q is constant and $r = 0$ (no acculturation). B depicts the effect of varying q (engagement), with constant $s = 10$, while C depicts the effect of varying s (assortment parameter), with constant $q = 0.5$. For each treatment, the results of five replicate runs are shown. Whole-population extinction at high levels of q has been prevented by enforcing fissions if the population drops to a single group.

acculturation), so that conflicts are always lethal for the losing group. The results show that even small amounts of engagement are sufficient to sustain high levels of warrior production (Fig. 1B). This occurs despite the fact that high levels of warrior production entail costs not only to the individual bearers of the trait, but also to their group (in the form of lower group sizes, which in turn reduce their fissioning rates). Thus [in contrast to previous models (3, 46)], warrior production is not necessarily a form of within-group (or “parochial”) altruism. Rather, the relative group-level benefits and costs of warrior production will depend on the state of the global population at any given time.

Contrary to what one might expect, it is not the case that higher amounts of engagement necessarily entail higher warrior production. The population equilibrium depends not only on the level of engagement, but also on the number and variance of groups, the group composition, the rates of fission and extinction, and the balance between individual- and group-level selection. For example, the number of groups and the between-group variance in mean p decrease with increasing conflict frequency, which decreases the effectiveness of group selection. Nevertheless, there is a minimum amount of engagement above which warrior production is favored.

Because the evolution of warrior production is a result of group selection, it depends on the maintenance of variability between groups. Without associative splitting (i.e., when $s = 0$), daughter groups have the same distribution in p as their parent groups. Therefore, although p can increase transiently (as long as standing variation exists), eventually between-group variation in p will be exhausted, and individual-level selection will dominate. Associative splitting ($s > 0$) prevents this outcome (Fig. 1C), with even modest amounts of assortment being sufficient to generate the evolution of at least some warrior production.

The Evolution of Warrior Production Can Lead to Whole-Population Extinction. Due to stochastic variations in the (finite) number of groups, the long-term demographic fate of the global population in our model is always extinction; nevertheless, the population will often persist for a long time in state in which the number of groups fluctuates stochastically around a predicted value (so-called “metastable” states, although here we refer to them, in slight abuse of terminology, simply as equilibria).

Assuming that the population is monomorphic in q (engagement), r (acculturation), and p (warrior production), and that

all groups have the same density $n(p) = x(p) + y(p)$, we can approximate the expected equilibrium number of groups \hat{N} (*SI Appendix, Eq. S7*). This approximation is not a quantitatively accurate estimate for the realized number of groups at any given moment (Fig. 2A, dashed line), due to the assumptions of monomorphic populations and identical groups. Furthermore, when p is evolving, the number of groups does not necessarily have time to reach the predicted equilibrium, especially when the number of groups is low. Qualitatively, however, our prediction agrees with the simulation data that the number of groups at equilibrium is a decreasing function of p (Fig. 2A). Thus, group selection favoring the production of warriors also results in a decrease, over time, in the number of groups at equilibrium. As a consequence, selection for increased p makes stochastic population-wide extinction increasingly likely. As shown in Fig. 2B, time to extinction decreases for higher warrior production.

In deterministic evolutionary models, the adaptive evolution of a population toward its own extinction is called evolutionary suicide (47, 48), also known as Darwinian extinction (49). Here, we have a similar (though not identical) process: the adaptive evolution of a population toward smaller and smaller sizes, increasing the risk that stochastic variations will cause whole-population extinction.

The process of evolution toward extinction has often been studied in the context of self-interested individuals destroying common resources, a scenario which could be averted by group selection (50). In contrast, our model provides an example of group selection causing (rather than preventing) evolution of a population toward extinction.

Without Acculturation, Intergroup Conflict Is Not Favored. In the previous section, we considered engagement to be a constant group trait. While this does not imply that conflicts occur at a constant rate (because group-interaction rates depend on the number of groups in the population), it means that groups have no control over how frequently they engage in them. In reality, not all human groups are likely to be equally prone to engage in conflict, which in our model corresponds to variation in the group trait q . We modeled this variation by characterizing groups with a trait q (engagement) that influences the frequency with which they initiate conflicts.

Groups with higher values of q engage in conflicts more often and, thus, are more likely to be eliminated from the population. Even high-engagement groups with higher numbers of warriors may be defeated stochastically. Furthermore,

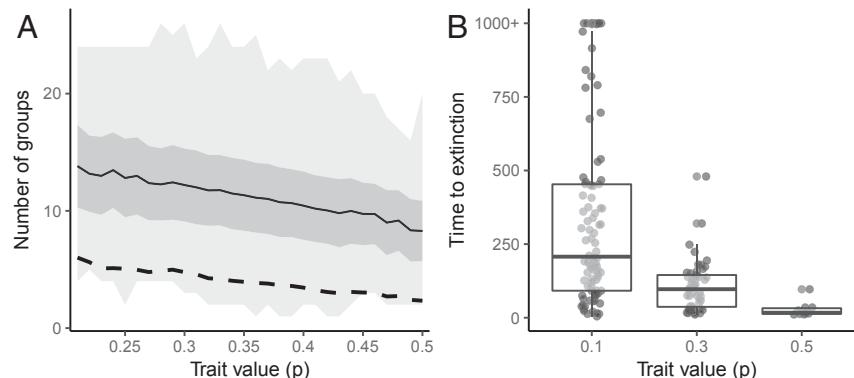


Fig. 2. Evolution of warrior production increases the risk of whole-population extinction. Increased warrior production leads to a lower number of groups, which decreases time to extinction. (A) Five replicate simulations with constant $q = 0.64$, $r = 0$ were grouped together to calculate mean group size for different values of mean group p . Dark ribbon shows standard deviations, and light ribbon indicates the full range of values. The dashed line shows estimated equilibrium values for group density [*SI Appendix, Eq. S7*, using mean group density in place of $n(p)$]. (B) Time to whole-population extinction (simulations were interrupted at time $t = 1,000$). For each value of p , we show 50 replicate simulations. All trait values (p , $q = 1$, and $r = 0$) were held constant.

defeating other groups does not increase a group's birth rate (i.e., fission rate), as would be the case if victories were associated with resource exchange. On the contrary, the groups that could conceivably benefit from higher engagement are those that have many warriors and, therefore, lower densities and fission rates. Therefore, although groups may produce warriors if conflicts are frequent, this is not an evolutionarily stable state, and groups that avoid initiating conflicts are more likely to persist and leave descendants. Thus, if winning group conflicts does not affect group birth rates, engagement (a group-level trait) and warrior production (an individual-level trait) coevolve toward a "peaceful equilibrium" (Fig. 3A), at which $q \approx 0$ and $p \approx 0$. (For more details, see *SI Appendix, section S4*.)

Acculturation Drives the Evolution of Intergroup Conflict. With acculturation, winning a conflict translates into a birth event for the winning group, because the loser of the conflict takes on the cultural traits of the winner. This turns out to tip the balance in favor of engagement: If conflicts are associated with the transmission of the victor's culture, rather than the elimination of the defeated group (i.e., if $r = 1$), engagement and warrior production coevolve toward frequent conflicts rather than peace (Fig. 3B). This occurs despite none of the individuals involved in the conflicts earning any reproduction-enhancing benefit.

Increased engagement does not provide either individuals or groups with any benefits, as it has no effect on the probability of surviving a conflict. In fact, q is released from selection when $r = 1$, since no groups are eliminated as a result of conflicts, which explains some of the fluctuations and high levels of variation in q (Fig. 3B; see also *SI Appendix, section S4*).

On the other hand, cultures that are simultaneously engaging and warrior-rich maximize their own replication through acculturation. The reason why being engagement-prone and having warriors is a successful strategy when there is acculturation can be understood based on the following argument. Consider a pop-

ulation of N groups in which a number of groups ν have a more engaging and warrior-rich culture than the other groups. A more engaging group tends to win a single encounter with a less engaging group. If the victory results in the elimination of the defeated group, the frequency of the high-engagement groups increases by $\frac{\nu}{N-1} - \frac{\nu}{N} = \frac{\nu}{N(N-1)}$. However, if the victory results in the defeated group taking on the culture of the victor, the frequency of the high-engagement group increases by $\frac{\nu+1}{N} - \frac{\nu}{N} = \frac{1}{N}$. Thus, the increase in frequency tends to be much larger with acculturation (up to about N times larger if $\nu \ll N$).

Thus, the evolution of engagement occurs due to cultural drive, rather than due to any adaptive effect on its host groups. Although the level of engagement fluctuates widely, and sometimes drops to low values, it is associated with an increase in warrior production, which rises to the value at which warrior density is maximized ($p \approx 0.514$). This is a stable and reliable indicator that the majority of groups are prepared for conflict.

Acculturation Coevolves with Engagement and Warrior Production. Finally, we consider the joint evolution of warrior production (p), engagement (q), and acculturation (r). Whereas the first trait characterizes individuals, the other two traits characterize groups. Starting from a peaceful population with small amounts of warriors or engagement, acculturation rapidly spreads, driving engagement and warrior production along with it (Fig. 3C). This occurs despite the fact that there are costs associated with high engagement: Namely, during the initial increase of the acculturation trait, there is a risk (with probability $1 - r$) that a defeated group will be eliminated from the population. Furthermore, as discussed above, there are also costs (at both the individual and the group level) associated with high warrior production. Nonetheless, p evolves to maximize warrior production ($p \approx 0.514$).

To understand the rise of acculturation, consider the fate of a group with a mutation in this trait (r'), in a population that

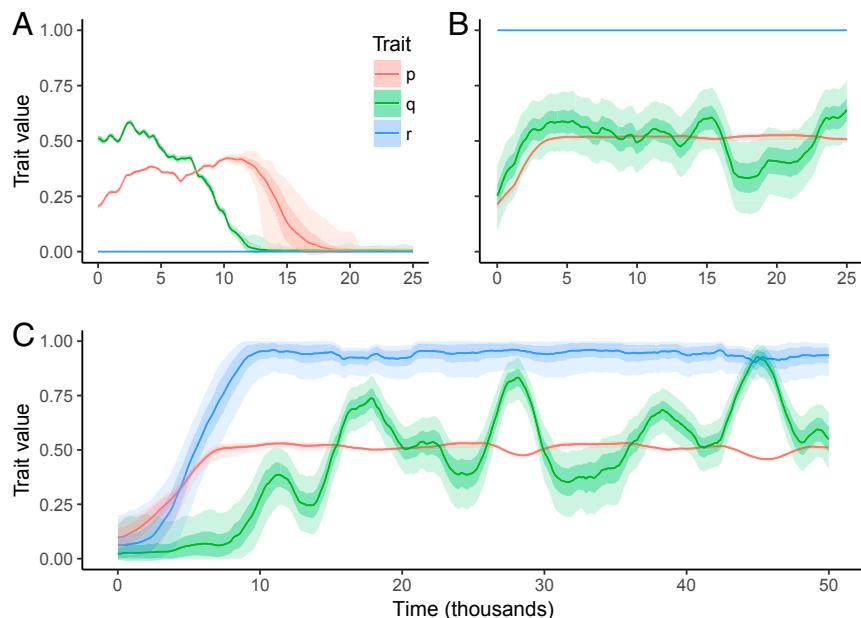


Fig. 3. Coevolution toward peace and coevolution toward conflicts. Time dynamics of a single replicate, showing the coevolution of the individual-level trait p (warrior production) and the group-level traits q (engagement) and r (acculturation). (A) Without acculturation ($r = 0$), q and p coevolve toward a peaceful equilibrium. (B) With maximal acculturation tendency ($r = 1$), q and p coevolve, leading to conflicts and maximizing warrior production ($p \approx 0.514$). (C) Acculturation coevolves with the other traits, resulting in an outcome similar to B. Lines indicate population-wide rolling averages of group values (q , r) or of mean group values (p). Dark ribbons show rolling standard deviations, and light ribbons encompass the full range of values. To make the transient dynamics of p and q clear, mutational effect sizes in A ($\sigma_q = 0.01$) are smaller than in B and C ($\sigma_q = 0.05$).

is monomorphic for the group trait values q and r . Furthermore, assume that the number of groups is large and has reached equilibrium (*SI Appendix*, Eq. S7). The only term in the group dynamics that depends on r' is the rate at which resident groups are defeated and acculturated. If the mutant group defeats resident groups with a probability g (independent of r' ; *SI Appendix*, Eq. S4), this rate is given by $G(q, N)r'g$. Since the mutant is rare, the corresponding rate for the resident r is $G(q, N)rg$, and, hence, the mutant's rate of winning is higher than the resident's if and only if $r' > r$. Thus, invasion dynamics favors larger acculturation values.

In summary, although the production of warriors and the evolution of conflicts are deleterious traits from the perspective of individuals, they are advantageous from the perspective of the cultural variants themselves, since warrior-rich and engagement-prone groups with high acculturation tendencies are more likely to succeed in spreading their cultural variants in the event of a group interaction.

Overview of Model Behavior and Robustness. So far, we described how multilevel cultural selection can drive the coevolution of acculturation, engagement, and warrior production for a particular set of parameters. In this section, we argue that the patterns we discussed are robust and general. Overall, there are three main categories of possible outcomes in this model. The first outcome, illustrated in Fig. 3C and discussed above, is “coevolution toward conflict,” where r approaches 1, p approaches the value that maximizes warrior density, and q evolves to intermediate values and experiences large fluctuations. (Of these traits, q is the most sensitive to changes in parameters; most of the regimes discussed below decrease the equilibrium level of q compared with Fig. 3C.) A second possibility is whole-population extinction, also discussed above. This outcome is expected if the fission rate is too small compared with the group extinction rate—i.e., for low group-growth rates.

The final possibility is that all traits evolve toward near-zero values (peaceful equilibrium). This will be the case if group selection is too weak relative to individual-level selection, which can occur, for example, if fission-associated assortment is absent (Fig. 1C). It can also occur if the frequency of group events is very low, because one basic requirement for the increase in warrior production is that group events should occur frequently enough relative to within-group population turnover (*SI Appendix*, section S3). Keeping all other parameters identical, we obtained a peaceful equilibrium once the group-event rates were three orders of magnitude lower than the reference parameters (*SI Appendix*, Fig. S6). Group selection will also be weaker if the number of groups is small, but our results are fairly robust to this aspect. Small numbers of groups can be obtained either by changing the individual-level rate parameters or by changing the group-level rate parameters. Within-group parameters that result in smaller groups will imply lower fissioning rates, and therefore fewer groups. In *SI Appendix*, Fig. S7A, the population evolves toward conflict, even though the individual-level parameters are such that the equilibrium number of groups is only about 24, an order of magnitude lower than in Fig. 3C (214 groups). Small numbers of groups can also be obtained by decreasing the fissioning rate. *SI Appendix*, Fig. S7B shows the dynamics of a population whose fissioning rate is one order of magnitude lower than the default parameter. Despite having only around 17 groups at equilibrium, it displays coevolution toward conflict. (Populations this small are at risk for population-wide extinction, a fate that was artificially averted in *SI Appendix*, Fig. S7B by preventing extinction when the population was down to one remaining group.)

Another potential challenge to coevolution toward conflict occurs when small increases in warrior production impose higher penalties on group size (and, by extension, on group fissioning

frequency). Although $\hat{n}(p)$ is a strictly decreasing function of p (*SI Appendix*, Eq. S5), its shape depends on the choice of parameters. In particular, the decrease in $\hat{n}(p)$ for small values of p may be either accelerating (if $2b_1 \leq d$) or decelerating (otherwise); *SI Appendix*, Fig. S2 A and B. Our reference parameters result in an accelerating function. Although decelerating functions pose higher challenges to any increase from low values of p (because they correspond to steeper reductions in group density), additional simulations (*SI Appendix*, Fig. S4) confirm that coevolution toward conflict is robust to decelerating functions.

Apart from changes to the main parameters of our model, we note also that the model is robust to generalizations. For example, coevolution toward conflict can still occur in the case of costly acculturation, in which a fraction of individuals die before acculturation (*SI Appendix*, section S5 and Fig. S5). This could correspond, for example, to scenarios in which one of the rival factions surrenders upon incurring some level of casualties. Another generalization is the case in which warriors can reproduce (*SI Appendix*, Fig. S8). In this case, warriors inherit their parent's trait value p . When they reproduce (at some fertility cost $c < 1$), this trait value determines (as it does in shepherds) the proportion of offspring that will become warriors. Predictably, reducing the cost of warrior production makes the evolution of warriors less stringent. Because warrior production imposes a smaller penalty on group size, the value of p at which warrior density is maximized is higher for lower values of c . Therefore, all else being equal, lower values of c lead to higher equilibrium levels of p .

Discussion

The most common explanation for the evolution and persistence of intergroup conflict in human societies is that their costs are compensated by the acquisition of reproduction-enhancing resources, such as food, mates, or territory, held by other groups (18, 19, 45, 51–53). Here, we have argued that the cultural evolution of conflicts can be explained, even in the absence of such benefits. As an alternative explanation, we showed that conflicts can be maintained by cultural drive. In analogy with meiotic drive, cultural drive is the process by which a cultural trait spreads by promoting its own transmission at the expense of its host's fitness. In our model, the particular mechanism underlying this process is acculturation: the imposition of the victor's culture on defeated groups following conflicts. Acculturation evolves as an alternative to direct elimination of defeated groups and paves the way for the evolution of group engagement and warrior production, ultimately resulting in the maintenance of intergroup conflict.

Because intergroup conflicts are best described as group-level events (rather than the sum of individual behaviors), our model explicitly tracks population dynamics at two levels (38). At the lower level, individuals are characterized by their tendency to become warriors. At a higher level, groups are characterized by social norms or institutions such as engagement (the tendency to engage in conflicts) and their tendency to acculturate defeated groups. The evolution of these traits is the result of state-dependent events at both levels: births and deaths for individuals, and fissions, extinctions, and conflicts for groups. Our assertion that intergroup conflict is a group-level event [i.e., an event that can potentially change the number of groups (38)] does not imply that the actual process (and its outcome) is not driven by the properties of individuals (namely, by the number of warriors within each competing faction, which is subject to cultural evolution). This is similar to the way group fissions are generated by individuals assorting themselves among daughter groups, so that their outcome will be determined by the trait distribution in the parent group.

Warrior production is necessary for winning conflicts, but it decreases the birth rate of individuals as well as the fission

rate of groups, and engagement increases the risk of group elimination by conflict. In the absence of acculturation—i.e., when conflicts always result in the elimination of the defeated group—the gain from victory in conflicts at the group level outweighs the cost of warrior production at the individual level if conflicts are certain to occur frequently enough. As Darwin speculated in *The Descent of Man*, when “tribes of primeval man, living in the same country, came into competition,” the ones with “disciplined soldiers” would “spread and be victorious over the other tribes” (54). Note that within each particular group, the relative frequency of shepherds still increases, since the gains that come from the presence of warriors (in this case, survival) are equally enjoyed by all group members. In this respect, participation in coalitional aggression is a collective action problem, where the lower fecundity of warriors is compensated by the (cultural) gains from competition with other groups. (This process is similar to ref. 55, where individuals who contribute to collective action at a cost have lower individual-level fitness compared with their noncontributing counterparts, but still increase in number because of the effects of intergroup competition.)

However, if engagement is itself a cultural trait of groups that evolves under group selection, the rate of engagement in risky conflicts evolves to zero, and, as a consequence, so does warrior production at the individual level. In the absence of acculturation, evolution will generate cautious, peaceful, and large groups with few warriors.

In contrast, with high acculturation tendencies, cultural variants that promote engagement get transmitted horizontally from group to group via group interactions, much like an epidemic spreads when its host interacts with other individuals. This leads to coevolution of engagement at the group level and warrior production at the individual level, the latter being selected by group selection despite still being disadvantageous at the individual level. Moreover, when acculturation is itself an evolving group trait, cultural group selection leads to high acculturation levels, ultimately resulting in populations in which conflict is common and warrior production substantial. Thus, our model shows that conflicts can become frequent, even when neither individuals nor groups benefit from it.

Previous models had already shown that the prevalence of intergroup conflict could potentially underlie the evolution of group-beneficial, but individually costly, human social behaviors (3), as well as the evolution of group-level social institutions through acculturation of defeated groups (4). Furthermore, past research had studied the coevolution of group-level institutions with individual social behaviors in the presence of intergroup competition (35). We extend this body of research by focusing on the origin of conflicts themselves and showing that, despite their costs, cultural group selection can favor their evolution when they are associated with the horizontal transmission of social behaviors and institutions.

In our model, acculturation tendency evolves to near one. At this point, very few cases of conflict are actually resolved with the death of defeated group members. This is (to some extent) reminiscent of modern wars in which casualties (relative to population size) are small (56, 57). Nonetheless, the results of the model are not contingent on the assumption that acculturation is a bloodless business, as illustrated by the case of costly acculturation (*SI Appendix, section S5*). Provided that group events are not too common, within-group dynamics eventually replenishes the defeated group’s warrior pool, rendering this type of demographic cost temporary.

If the birth rate of warriors is equal to or higher than that of shepherds, the conflict between individual- and group-level selection vanishes in our model, and the production of warriors will always be favored. Thus, in our context, interesting questions only arise when warriors have a lower birth rate, and, to

gain conceptual clarity, we assumed the worst-case scenario of no warrior reproduction for most of the analysis. In real human societies, costs of warriors are unlikely to be that extreme, but may be present nevertheless, e.g., in the form a direct risk of injury or death (increases in death rate), as well as time and energy investments or social conventions that may be associated with decreases in birth rate. For example, in ancient Sparta, the members of the privileged Spartiate warrior caste tended to marry late, leading to low birth rates (58). As an alternative biological interpretation, one can instead consider the cultural trait p to be the fraction of lifetime that individuals are expected to dedicate to warrior activity (such as a military service during which individuals refrain from reproduction). There is also a possibility that warriors may reap direct benefits from conflicts and even achieve higher reproduction than other individuals. For example, among the Yanomamö (an indigenous population living in the northern portion of the Amazon basin), men who kill an enemy during a raiding party may acquire a special status known as *unokai*. Across all age cohorts, *unokai* men have higher reproductive success than their non-*unokai* counterparts, due to their increased success in finding mates (14) (although reproductive success only seems to be measured among successful *unokai*, i.e., excluding the individuals who die in the attempt to achieve that status). Similarly, among the Nyangatom, a group of nomadic pastoralists in East Africa, men who acquire livestock through raiding have higher access to reproductive opportunities, since Nyangatom marriage traditions require the exchange of bridewealth. Thus, Nyagatom elders who participated in raiding in their youth tend to have more wives and children than other elders (15). In cases like these, in which benefits outweigh the costs, individual-level selection alone is capable of explaining the production of warriors.

It would be extremely speculative to suggest that acculturation is anything more than a partial driver for the prevalence of intergroup conflict in actually existing human societies. A complete picture of the origin and maintenance of conflict must also incorporate individual-level benefits, such as the acquisition of territory, access to females, or food (18, 45, 52, 53), as well as the ways in which individual benefits may feed back into group-level events by increasing the chances of victory (19). Nonetheless, the idea that cultural evolution may promote the spread of conflict, even in cases where it may be maladaptive, has received relatively little attention. Conceptually, this type of explanation broadens the conditions under which we expect conflicts to occur, thus adding to, rather than replacing, current explanations. Perhaps in the future, a combination of both approaches will yield additional insights. For example, the dynamics of group size and number may in turn affect individual-level payoffs.

Our model is, of course, not meant as a rigorous characterization of any particular human society or moment in human history. Understanding the extent to which our results apply to, for example, hunter-gatherer societies, would require parameterizing our model with anthropological data and expanding it to include other relevant demographic processes such as migration and resource dynamics, as well as sexual reproduction. This would be a challenging task that we did not attempt to undertake. Our model is also unrealistic in considering primarily large-scale battles that result in the massacre of the defeated group, an outcome that, in hunter-gatherer conflicts, was usually limited to cases in which one side was greatly outnumbered (59). Nonetheless, our model illustrates the possibility that, even in the absence of conflict-associated benefits, we can generate the same observed patterns as predicted by the resource-based, adaptive hypothesis that is paradigmatic in cultural evolution and biology. Importantly, the central ingredients of our explanation—social institutions and their horizontal transmission between groups—rely on uniquely human cognitive capacities and therefore

suggest a qualitative difference between the causes of human and nonhuman intergroup conflicts. This is in contrast with a long-standing tradition in biology of proposing an evolutionary continuity between antagonistic behavior in human and nonhuman animals (9).

Although we didn't explore them in our model, it would be interesting to investigate the effects of other types of events. For example, migration between groups, or even group fusions, could lower intergroup diversity and reduce the effect of group selection. Furthermore, although we have framed our model in terms of the evolution of human conflict, the same concepts and methods could be used to address other questions in cultural evolution. "Warrior production" in our model is an archetype for any institution or cultural practice in which societies invest costly resources for the purpose of succeeding during group interactions. In the same way, our modeling framework could accommodate other types of group interactions, including mutually beneficial ones such as trading, which can provide a different mechanism for the horizontal transmission of cultural variants between groups. Traditional (one-level) cultural evolutionary game theory has shown that costly behaviors (such as cooperation) can persist thanks to the frequency-dependent effects of interactions between individuals, provided that traits are transmissible [social learning (60)]. A multilevel framework for cultural evolution allows us to apply the same logic to the persistence of costly practices via their effect on interactions between groups, provided that these practices are transmissible (acculturation). We expect that this approach can yield insights much beyond the scope of human warfare, such as the cultural evolution of religion (61).

Materials and Methods

To simultaneously model evolution at two levels, we simulate within-group dynamics deterministically (as a system of differential equations), while modeling between-group dynamics stochastically (as a Markovian process). Thus, our implementation follows a hybrid (partly deterministic, partly stochastic) method to simulate group-selection dynamics (62, 63).

At the within-group level, the model is implemented by discretizing the trait space into k bins and tracking the density x_i of shepherds of type p_i , $1 \leq i \leq k$. Since warriors do not reproduce, there is no need to keep track of their trait value (but the extension to the case when warriors also reproduce is straightforward). This results in a system of coupled differential equations:

$$\dot{x}_i = \left(\sum_{j=i}^k \mu_{ij} x_j (1 - p_j) - \sum_{j=1}^k \mu_{ji} x_i (1 - p_i) \right) b(X, y) - x_i d, \quad [3]$$

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$$\dot{y} = \sum_{i=1}^k x_i p_i b(X, y) - y d,$$

where μ_{ij} is the mutation rate from trait value j to i (with μ_{ii} being the probability of no mutation), and $X = x_1 + x_2 + \dots + x_k$. This system of equations is solved numerically in small time increments dt using the Euler method.

While the densities within each group are updated deterministically, group events occur stochastically based on their rates. The time increments dt are assumed to be small enough that the occurrence of more than one group event per increment is unlikely. The total group rate (T) is given by the sum of all group-event rates; the probability that a group event will occur in a given increment is then $T \times dt$. The particular event type and the focal group are determined by weighted lottery, with probabilities proportional to the different group-event rates.

The relative velocity of the two time scales (group selection and individual selection) can be regulated by adjusting the rate constants (ε , ϕ , and γ). Multiplying them by a common factor regulates the overall frequency of group events and, hence, the relative strength of group selection vis-à-vis individual selection.

In the event of an acculturation, the relative densities $x_i/(X + y)$ of the defeated group were changed to match those of the victor, while keeping the total density ($X + y$) constant (where $X = x_1 + x_2 + \dots + x_k$).

Default Parameters. In the numerical examples and figures throughout this work, unless otherwise stated, we used the following parameter values.

For the individual-level rates, we used the parameters $b_1 = b_3 = 0.1$, $b_2 = 3$, and $d = 0.5$; additional simulations show that the qualitative results of the model are robust to the changes in group size that may result from small deviations from these values. This is because changes in group size (which affect the intensity of individual-level selection) also lead to changes in the equilibrium number of groups (which affects the intensity of group selection).

For the group-level rates, we used the parameters $\varepsilon = 0.025$, $\phi = 0.05$, and $\gamma = 0.05$. Variations about these values have no qualitative effect on our results, provided that large changes in the frequency of extinctions or interactions are compensated by adjustments to the fission rate, and vice versa (to avoid extinction of all groups).

Additional parameters were as follows: $s = 10$, $g_s = 10^{-4}$, $\iota = 10^{-5}$, $\sigma_q = \sigma_r = 0.05$, $k = 101$, and $dt = 0.01$. The mutation rate was $\mu_{ij} = 0.01$ if $i = j \pm 1$, otherwise zero. The results we show are typical for the vicinity of these parameter values.

Language and Data. The simulations were performed in Matlab (Version R2017a) (64) and the analyses and figures with R (Version 3.3.2) (65). Simulation code and data have been deposited in GitHub (66).

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