

- Holocene. However, CH₄ emissions are not well known for lakes in these regions and are not included in our thermokarst-lake CH₄ emission estimate. Our calculations of CH₄ emission from thermokarst lakes are based on a conservative estimate of the extent of yedoma, namely its current distribution in north Siberia and the previously exposed adjacent continental shelves (total area: 1.9 × 10⁶ km² at 15 kyr B.P.). Additional details are provided in the SOM Materials and Methods.
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Supporting Online Material

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The Coevolution of Parochial Altruism and War

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Altruism—benefiting fellow group members at a cost to oneself—and parochialism—hostility toward individuals not of one’s own ethnic, racial, or other group—are common human behaviors. The intersection of the two—which we term “parochial altruism”—is puzzling from an evolutionary perspective because altruistic or parochial behavior reduces one’s payoffs by comparison to what one would gain by eschewing these behaviors. But parochial altruism could have evolved if parochialism promoted intergroup hostilities and the combination of altruism and parochialism contributed to success in these conflicts. Our game-theoretic analysis and agent-based simulations show that under conditions likely to have been experienced by late Pleistocene and early Holocene humans, neither parochialism nor altruism would have been viable singly, but by promoting group conflict, they could have evolved jointly.

Late 19th-century scientists as diverse as Charles Darwin (1) and Karl Pearson (2) recognized war as a powerful evolutionary force that might foster social solidarity and altruism toward the fellow members of one’s group. But despite Hamilton’s speculation about how this could occur (3), neither the process by which war might have become sufficiently common to support the evolution of altruism nor the possibility that altruism conditioned on group membership might have contributed to the unusually high level of lethal intergroup conflict among humans has been subjected to systematic investigation.

The empirical importance of both altruism and hostility to members of other groups is well established. Experimental and other evidence demonstrates that individuals often willingly give to strangers, reward good deeds, and punish individuals who violate social norms, even at a substantial personal cost (4), while favoring fellow group members over “outsiders” in the choice of friends, exchange partners, and other associates and in the allocation of valued resources (5). For example, a recent “third party punishment” experiment in Papua New Guinea revealed strong favoritism toward a subject’s own linguistic group in giving to others, and significantly greater punishment of individuals from another linguistic group (by comparison to the subject’s own group) who acted ungenerously toward the subject’s fellow group members (6).

Intergroup hostility and aggression are similar to altruism in that an individual adopting these

behaviors incurs mortal risks or foregoes beneficial opportunities for coalitions, co-insurance, and exchange, thereby incurring a fitness loss by comparison to those who eschew hostility toward other groups. When this is the case, and when the members of the actor’s group benefit as a result of one’s hostile actions toward other groups, we term the behavior “parochial altruism.” The experimental subjects in Papua New Guinea provide an example.

Neither parochialism nor altruism would seem likely to survive any selection process that favors traits with higher payoffs. But parochial altruism could have emerged and proliferated among early humans because our ancestors lived in environments in which competition for resources favored groups with substantial numbers of parochial altruists willing to engage in hostile conflict with outsiders on behalf of their fellow group members. These group benefits could have offset the within-group selection against both parochialism and altruism. Unlike multilevel selection models in which group conflict is simply assumed (7–9), we thus provide an explanation of warfare itself and its uniquely lethal nature among humans. Whether this account is plausible is an empirical question.

The ethnographic and archaeological record suggests that warfare was a frequent cause of death among some hunters-gatherer groups and early tribal societies (10, 11). Mortality in intergroup conflicts as a fraction of all deaths may have been an order of magnitude greater among early humans than among Europeans during the bellicose 20th century. Most hostile intergroup contact was probably ongoing or intermittent, with occasional casualties, more akin to boundary conflicts among chimpanzees (12) than to modern warfare. However, “pitched battles” did occur

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among foragers, as in the conflict between two coalitions of aboriginal Australians involving around 700 combatants (13). As natural disasters and periodic resource scarcity have been identified as the most important correlates of warfare among forager groups (14), it seems likely that the volatile climate of the late Pleistocene (from about 125,000 until 10,000 years before the present) contributed to high levels of intergroup conflict. Groups that avoided hostile interactions benefited from greater access to the resources in what would otherwise have been nonproductive defensive buffer zones (15, 16), as well as from between-group risk sharing (17) and exchange (18), often over substantial distances [see also (19)].

Could parochial altruism have emerged and proliferated in this environment? We model the evolution of genetically transmitted behavioral types in a population of foragers who engage in both within- and between-group interactions. Individuals may be altruistic (or not) and parochial (or not). We represent these behaviors as the expression of two hypothetical alleles at each of two loci. There are thus four types: parochial altruists (PA, that is bearers of the P and A alleles), tolerant (nonparochial) altruists (TA), parochial nonaltruists (PN), and tolerant nonaltruists (TN). Parochials (of either type) are hostile toward other groups. But only parochial altruists engage in combat, because the nonaltruists are not willing to risk death in order to benefit their fellow group members. In the absence of between-group hostility, tolerant members of a group benefit from the above-mentioned mutually advantageous interactions with other groups.

Two types of selection are at work in the model to be presented. Within-group selection favors tolerant nonaltruists and tends to eliminate parochial altruists (as well as tolerant altruists and parochial

nonaltruists). By contrast, the second process, selective extinction resulting from intergroup conflict, may favor parochial altruists despite the fact that they risk death even in victorious battles. To clarify the role of war, parochialism, and selective extinction, we do not model the other mechanism by which altruism may spread, namely, selective emigration (20). Thus, in the absence of territorial expansion through conquest, we assume that group size is fixed, so highly altruistic groups do not contribute more replicas to the next generation. Our setting, therefore, is quite unfavorable for the evolution of altruism because it is equivalent to models in which local density-dependent selection exactly offsets the group benefits of altruism (21, 22).

Parochial altruists who survive conflicts do receive a direct individual reproductive benefit if a war occurs, because they share in their group's increased probability of winning a hostile encounter that results from their status as a "fighter" (relative to the expected outcome of the conflict had the individual been of another type). Winning a hostile encounter yields two kinds of reproductive benefits for members of a group: a greater chance of survival and (for the survivors) the opportunity to produce additional offspring to replace those killed in the losing group. However, in our simulations (19), the increased risk of mortality in warfare incurred by parochial altruists offsets this direct benefit by a wide margin. As a result, each parochial altruist would enjoy substantially greater expected reproductive success by switching to tolerant and/or nonaltruistic behaviors, even taking into account that the switch would increase the probability that his group would be defeated should a conflict occur. Thus, those who fight for their group are altruistic in the standard sense of the term (23).

Every generation, all members of each group are paired randomly with members of their group to produce offspring, whose expected number is proportional to the parental couple's share of the group's payoffs, described below. So as not to favor the hypothesized coevolution of parochialism and altruism that depends on the two behaviors being statistically associated, we adopt an intergenerational transmission process with no built-in tendency for the parochial and altruistic alleles to be correlated. Thus, we assume no within-group assortment in mating and we allow complete recombination (so that, e.g., a parental couple composed of a PA and a TN will have offspring of all four behavioral types with equal probability). Additionally, this process is modified by mutation: With some probability (μ), each member's offspring inherits a type randomly from the four possible types independently of the parental types. With probability $(1 - \mu)$, the nonmutational replication above takes place. Each generation, with some probability (m), each member migrates to a randomly selected group.

Between-group interactions are as follows. Every generation, each group interacts with another group either cooperatively or in a hostile manner (Fig. 1). Hostility in an intergroup interaction results if the fraction of parochial members of at least one group is sufficiently great. The use of force between the two groups occurs when one of the two is sufficiently likely to win, reflecting the fact that as with other primates, evenly matched human groups seek to avoid costly conflicts (24). The probability that a group wins a conflict depends on the difference in the number of fighters (parochial altruists) in the two groups. If a conflict occurs, a fraction of the fighters in both groups die, and a fraction of the surviving fighters and nonfighters of the losing group are also eliminated. This civilian mortality fraction is equal to a constant times the between-group difference in the fraction of parochial altruists, so the greater is the imbalance of forces, the more severe are the fatalities of the losers. If the group with more fighters does not win, the outcome is a draw in which fighters die as above, but nonfighters do not.

Those eliminated in both groups are replaced by offspring from randomly chosen mates (as described above) in the winning group, who migrate to the losing group, bringing both groups' numbers up to the capacity of their sites. We explored (19) an alternative to this "migration" scenario in which the fighters of the winning group kill fewer of the losers but mate with the surviving losing population, repopulating their site in this manner. This "mating" scenario favors the evolution of parochial altruism more strongly than the results shown below as it privileges parochial altruists (because they are the fighters who mate with the losing population) in the repopulation process (by comparison with the migration scenario, in which those parenting the colonists to repopulate the losers' site are drawn randomly from the survivors among the winning population).

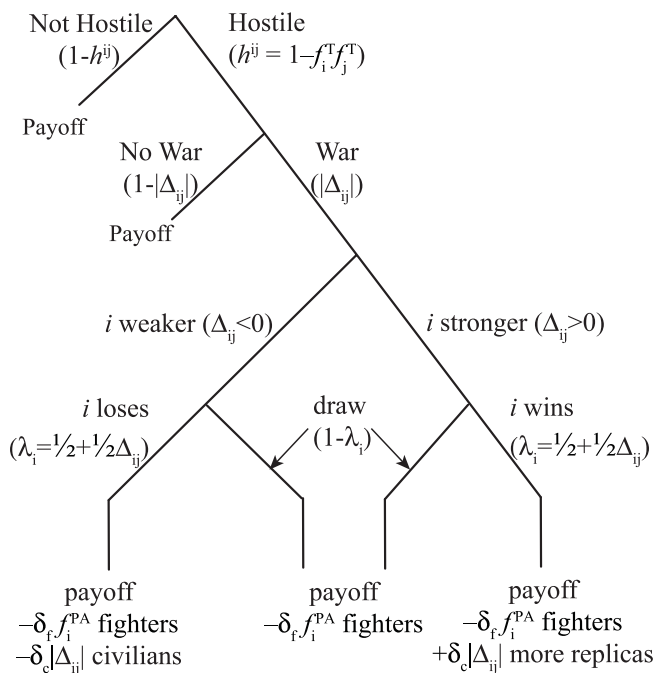


Fig. 1. Between-group interaction. Notation: f_i^T, f_j^T = the fractions who are tolerant in group i and group j , respectively; $h^{ij} = 1 - f_i^T f_j^T$ = the probability that an interaction between groups i and j will be hostile; f_i^{PA}, f_j^{PA} = the fractions who are parochial altruists in group i and j ; $\Delta_{ij} = f_i^{PA} - f_j^{PA}$; $|\Delta_{ij}|$ = probability that a hostile interaction will result in a war; λ_i = the probability that group i wins the war; δ_f = the fraction of fighters (PAs) who die should a war occur ($\delta_f = 0.14$ in our benchmark simulations) and $\delta_c |\Delta_{ij}|$ = fraction of civilian mortality in the losing group ($\delta_c = 2.5$ in our benchmark simulations). Payoff refers to the payoffs to the public goods and peaceful intergroup interactions described in Table 1.

If the interaction is not hostile, each tolerant member receives a net benefit from each tolerant member of the paired group. Parochials receive no such benefits. As a result, in the absence of hostility, the expected payoff to the Ts in a given group exceeds that to the Ps irrespective of the fraction of Ts in the group, so T is the dominant strategy.

Individual payoffs from within-group interactions are determined as follows. In every generation at a cost c , altruists contribute to a public good whose value (b) is shared equally among the n group members belonging to a single generation. The public good may be shared information, risk-pooling, or similar behaviors. Those who are not altruistic (Ns) do not contribute. Because $b > c > b/n$, contributing raises group-average payoffs; but a contributor's payoff would be increased by an amount $c - b/n$ by not contributing, irrespective of the number of other As within the group. The result is that both As and Ps face adverse within-group selection. These payoffs are described in Table 1.

The sequence of events in each generation is as follows: Group interaction occurs, followed by repopulation of any group that suffered fatalities in warfare; members of the reconstituted groups then interact in the public goods game, after which they reproduce in proportion to their share of the group's total payoffs in the game (couples producing an average of two surviving offspring so as to maintain group size); finally, the parental generation dies and migration of the new generation occurs.

Our agent-based computer simulation explored the properties of this model under a range of parameters calibrated to resemble the environment of most late Pleistocene and early Holocene (i.e., prior to about 7000 years ago) humans (19). Our benchmark group size ($n = 26$ members of a single generation or a total size of about 78) could represent a coalition of three bands, each of a total size likely to have approximated a late Pleistocene band (25). The benchmark migration rate (25% per generation) is based on observed hunter-gatherer population movements. Our metapopulation is composed of 20 groups, giving it a total size thought to be common among late Pleistocene ethno-linguistic units.

Figure 2A gives an approximation of the explicit dynamics of the underlying Markov process, the arrows indicating selection against parochials in the absence of altruists and conversely, as expected. Figure 2B shows that as a result of this dynamic, over a very long period, the simulated population spends most of the time in states with many parochial altruists and few of the other three types, or in states with many tolerant nonaltruists and few of the other three types. In the former case, high levels of parochialism promote frequent conflicts, the victors being those groups with many parochial altruists. By contrast, when tolerant nonaltruists are prevalent, hostilities are rare, the benefits of cooperative between-group interactions are substantial, and the within-group selection pressures against parochials and altruists therefore predominate.

Statistical analysis of very many generations in which the population is near point b in Fig. 2A

indicate that both altruism and parochialism are sustained by levels of intergroup conflict and deaths in warfare that are considerably below estimates from archaeological and ethnographic data relevant to late Pleistocene and early Holocene conditions (19). In the bellicose states near point b in Fig. 2A, 3.6% of the total population perish each generation in warfare, compared to an estimate of more than three times this number based on ethnographic and archaeological evidence (11). Our results thus do not require implausibly high levels of war-induced mortality.

The top and middle panels of Fig. 3 illustrate transition processes between states close to point a and those close to point b. These infrequent and abrupt transitions occur in both directions because, as a result of the random nature of matching of mates and groups, outcomes of group interactions, migration, and mutation, the population may move from the neighborhood of either point a or point b to a state where the selective forces represented by the arrows in Fig. 2A carry the population to the opposite corner of the state space. The bottom panel is a summary of states in a large number of runs. As seen in the bottom left panel, when parochial altruists are prevalent in the population, fewer wars occur because groups tend to be evenly matched. The bottom right panel shows that when wars are more frequent, there tend to be more parochial altruists in the population.

Experiments with alternative parameter values (19) show that the population frequency of parochial altruists and the incidence of deaths due to war vary inversely with group size and the migration rate. This is because these population structure parameters diminish the between-group differences in the distribution of types, thereby both reducing the frequency of wars and weakening the effects of selective extinction when wars do occur. War deaths and the population frequency of parochial altruists vary positively with the extent of losses inflicted on civilians among the losers. Varying the rate of mortality among fighters first increases the fraction of war deaths and then lowers it, because for very high rates of fighter mortality few parochial altruists survive in the population and few wars occur. The results are not very sensitive to plausible variations in the benefits and costs of altruism.

These results do not occur because parochial altruists directly benefit by increasing the chance that their group will prevail in a contest, as we have seen. Indeed, at most states, an individual who hypothetically switched to become a PA would incur a fitness loss larger than the cost (c) of contributing to the within-group public goods game. Nor do the two stable states (points a and b in Fig. 2A) arise because parochial altruists and tolerant nonaltruists deliberately associate with like types, as in the Eshel and Cavalli-Sforza model of "selective assortment" (26). Preferential assortment with close genetic kin is not involved, because groups are quite large and both migration and within-group pairing for reproduction are random.

Rather, the crucial assortment processes that account for our results arise endogenously from

the pattern of intergroup relationships. When cooperative interactions among groups are common, tolerant nonaltruists proliferate because they benefit from positive assortment when groups interact (because the pairs of groups that cooperate are those in which both have many tolerant members). Correspondingly, wars are characterized by negative assortment benefiting parochial altruists because evenly matched groups avoid wars, and the wars in which most parochial altruists engage (and win) tend to be against groups with larger fractions of the other three types. Thus, the enhanced reproductive success due to increased group success in war that a parochial altruist confers on his group-mates tends to disproportionately benefit other parochial altruists, explaining their success.

We have shown that transitions from tolerant nonaltruistic and hence relatively peaceful states to parochial altruist and bellicose states can be very rapid (occurring in less than 200 generations, or about 5000 years) (Fig. 3). The markedly higher reproductive success of predominantly parochial altruist groups when interacting with groups with fewer parochial altruists could therefore explain the rapid range expansions that are thought to be common among some late Pleistocene human groups, and thus may partly explain the still puzzling second great hominid diaspora that swept from Africa as far as Australia in the course of no more than 10 millennia.

The coevolutionary dynamics of parochial altruism and war outlined here also provide a plausible explanation of the results of the behavioral experiments such as the one in Papua New Guinea mentioned above. On the basis of our model, one would expect tolerant altruists to bear costs in order to give to both insiders and outsiders, and to punish those who violate norms. In view of the importance of mutually beneficial intergroup relations, punishment of norm violators by altruists would include out-group members as well as insiders. But parochial altruists would give preferentially to their own members and punish those who harm group members more severely than if the victim is not an insider. Our model thus shows that spiteful behavior toward outsiders and the other behaviors in the experiment could have evolved by benefiting other group members when hostile intergroup contests occur. (In the experiment, punishing an outsider increases the relative payoffs of the actor's group because the cost to the target is three times the cost to the punisher.) Giving to others in the experiment—even to one's own group members—cannot be explained by kin altruism because the cost of giving was the same as the benefit to the recipient; so this kind of behavior would not be selected for even if group members were identical twins.

Finally, the model and simulations contribute to an emerging evolutionary explanation of why group boundaries so powerfully influence human behavior (27–29).

We have explained how *Homo sapiens* could have become a warlike yet altruistic species. But there is no evidence that the hypothetical alleles

Table 1. Expected payoffs to four behavioral types: Public goods and peaceful intergroup interactions. The fraction of group i who are altruists is f_i^A . All members receive the benefit of the public good, bf_i^A . Tolerant players of both types receive the benefits of nonhostile group interaction, gnf_i^T , where g is the benefit of nonhostile group interaction, n is group size (of a

single generation), and f_j^T is the fraction of the other group who are tolerant. If the interaction is hostile, the bold entries do not apply; if no war occurs, the payoffs to parochials and tolerants are identical. Simulation benchmark values of the parameters in the table are as follows: $c = 0.01$, $b = 0.02$, $g = 0.001$, $m = 0.25$, $\mu = 0.005$, $n = 26$.

	Parochials	Tolerant
Altruist	$bf_i^A - c$	$bf_i^A - c + gnf_j^T$
Nonaltruist	bf_i^A	$bf_i^A + gnf_j^T$

Fig. 2. Parochial altruist and tolerant nonaltruist outcomes occur with high frequency. The parameter values are as in Table 1 and Fig. 1. (A) Each vector represents the expected change at each state, based on a transition matrix recovered from the underlying perturbed Markov process on the basis of 5 million observations from 10 runs of 5000 generations starting at each of the 100 states as described in (19). Longer arrows reflect a higher net transition probability from each state. Stable states (i.e., states at which the population will spend the most time under the dynamic given by our model) occur where both frequencies are ~15% (point a) and both ~85% (point b). Point c is a saddle (unstable critical point). (B) The height of the bars gives the long run fraction of time in which we observe the indicated pair of population-level frequencies of altruists and parochials in the population.

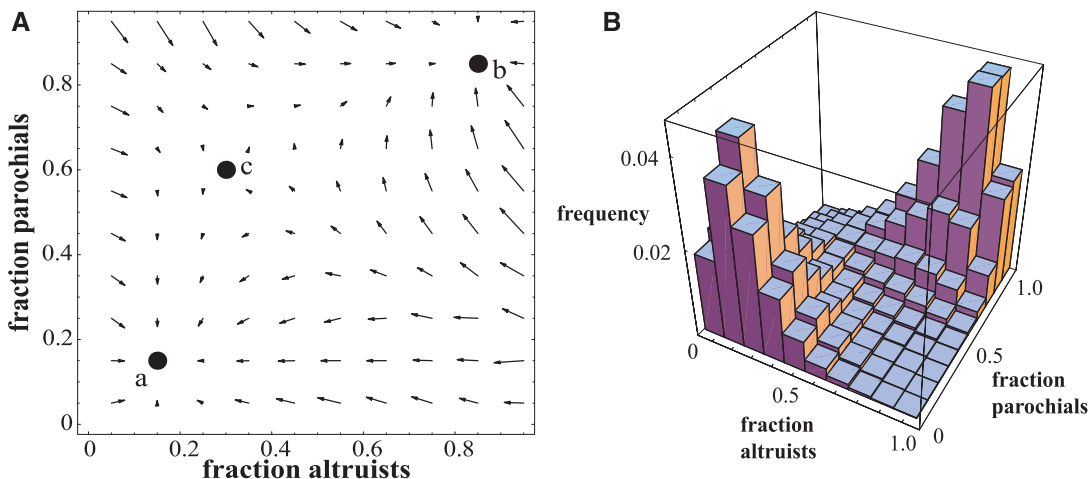
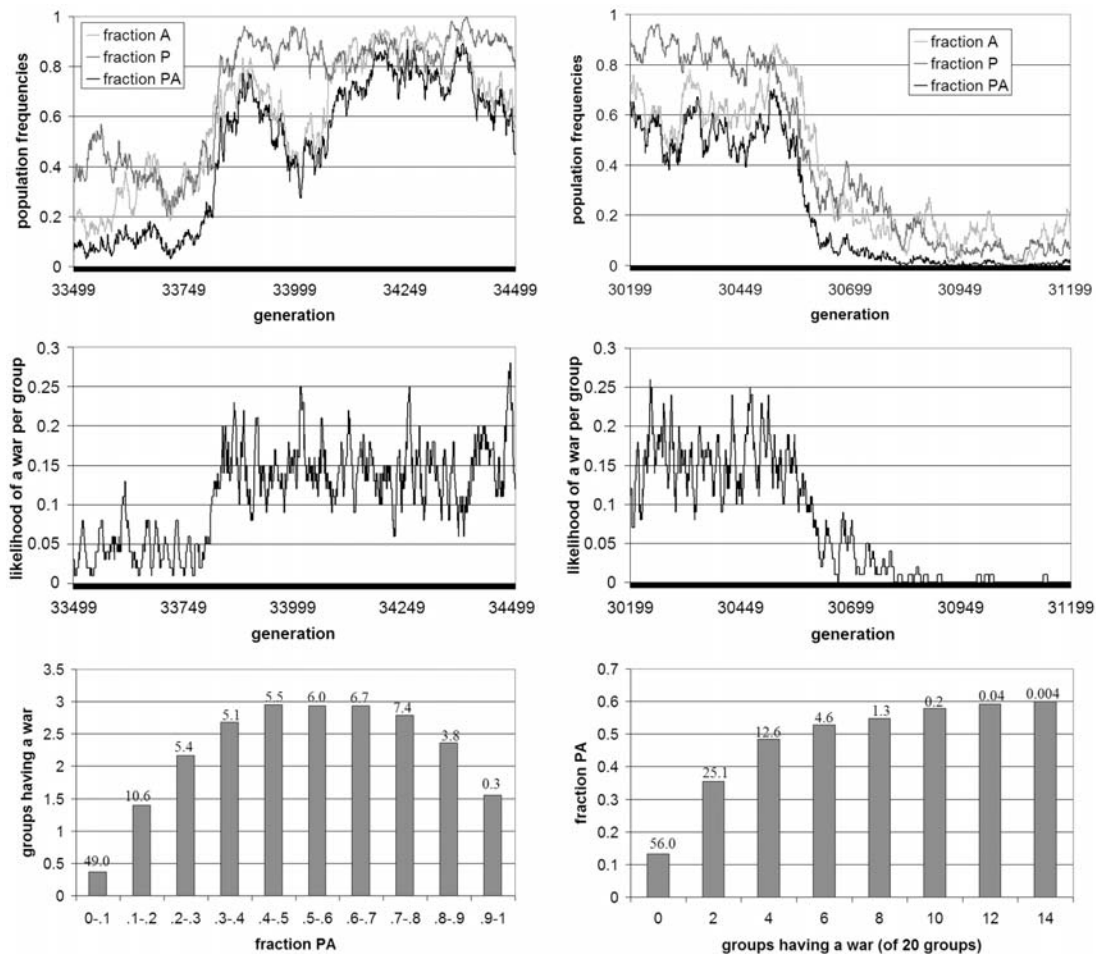


Fig. 3. Transitions between peace and war. The left panels in the top and the middle row illustrate a transition from a state near point a to one near point b in Fig. 2A. The right panels in the top and middle row show a reverse transition. Near point b in Fig. 2A, two-thirds of the population are PAs on average, and three-quarters of group interactions are hostile. Near point a, these figures are 4% and 24%, respectively. The bottom panels show that high frequencies of parochial altruists in the population sustain high frequencies of warfare and vice versa. Wars are most frequent when 40 to 70% of the population are parochial altruists (because at these frequencies imbalances between groups are more common). The numbers at the top of each bar indicate the percentage of 50,000 generations in which this fraction of PAs and this many wars occurred.



in our model exist, or that were they to exist they could be expressed in the complex behaviors involved in helping others and engaging in lethal conflict. Thus, we have not shown that a warlike genetic predisposition exists, only that should one exist, it might have coevolved with altruism and warfare in the way that we have described.

The vertical (parent-to-child) genetic transmission process in the model could be modified to encompass cultural learning processes and incorporate influences of peers and nonparental adults as well as parents. This extension would be essential if inferences about contemporary behavior are to be drawn from the model, for there is ample evidence that human parochialism can be readily redirected and even overridden by deliberate teaching, accidental exposure, and other aspects of socialization.

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Nanomechanical Basis of Selective Gating by the Nuclear Pore Complex

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The nuclear pore complex regulates cargo transport between the cytoplasm and the nucleus. We set out to correlate the governing biochemical interactions to the nanoscopic responses of the phenylalanine-glycine (FG)-rich nucleoporin domains, which are involved in attenuating or promoting cargo translocation. We found that binding interactions with the transport receptor karyopherin- β 1 caused the FG domains of the human nucleoporin Nup153 to collapse into compact molecular conformations. This effect was reversed by the action of Ran guanosine triphosphate, which returned the FG domains into a polymer brush-like, entropic barrier conformation. Similar effects were observed in *Xenopus* oocyte nuclei in situ. Thus, the reversible collapse of the FG domains may play an important role in regulating nucleocytoplasmic transport.

Nuclear pore complexes (NPCs) regulate nucleocytoplasmic transport (NCT) across the nuclear envelope (1–3). Each vertebrate NPC is a ~120-MD supramolecular assembly comprising ~30 different proteins, known as nucleoporins, that surround a central pore ~40 nm in diameter (4). The nucleoporins that are implicated in NCT are generally located near the nuclear and cytoplasmic peripheries of the NPC (5) and consist of natively unfolded domains rich in Phe-Gly repeat mo-

tifs (i.e., FG domains) (6). FG domains exhibit a functional redundancy (7) in terms of their binding promiscuity to transport receptors known as karyopherins (Kaps; also called importins and exportins) (8), which are required to facilitate NCT of specific cargos greater than 40 kD in size (but smaller than the pore diameter) (9). In the absence of Kaps, the FG domains impose a physical barrier that impedes the passage of macromolecules through the NPC (5, 10).

The dualistic functionality of the NPC, termed selective gating, is not strictly governed by size exclusion but exhibits a relative porosity that depends on the biochemical interactions involved during NCT. However, difficulties in directly visualizing the FG domains and their functional behavior in vivo (4) have allowed only figurative descriptions of Kap movement, such as “stepping from one FG-repeat to the next” (11),

“sliding over oily spaghetti” (12), or “sliding over a surface comprised of FG-repeats” (13). Alternatively, the FG domains may resemble a gel-like “selective phase” within which only Kaps stay soluble and can “melt” through (10, 14). Hence, the question remains as to how Kaps physically affect the FG domains to facilitate transport across the NPC.

To correlate the barrier-like behavior of the FG domains vis-à-vis Kaps, we covalently tethered the FxFG repeat-rich domain of Nup153 via terminal cysteines (i.e., Cys-hNup153-C or cNup153) to gold “nanodots” ~100 nm in diameter (15) (Fig. 1A). This allowed us to replicate a number of contextual details of the NPC: (i) FG-domain behavior in the NPC occurs at nanoscopic length scales; (ii) each FG domain is anchored at one end to the NPC while the other end dangles out into solution, rather than freely floating in solution; and (iii) a limited number of FG domains are confined to each NPC. Atomic force microscope (AFM) measurements provided the spatial distribution of the measured forces with respect to a cNup153-tethered nanodot (fig. S1). In the absence of karyopherin- β 1 (Kap β 1, also called importin- β), the cNup153 molecules exhibited a long-range steric repulsive force (Fig. 1A), which indicated that they were in a polymer brush-like, entropic barrier conformation (15).

Changes in the response of cNup153 were obtained by monitoring the brush height L_{exp} , decreasing from 29.1 nm \rightarrow 17.9 nm \rightarrow 13.7 nm \rightarrow 11.3 nm as the Kap β 1 concentration was increased from 0 \rightarrow 115 fM \rightarrow 2.5 pM \rightarrow 33 nM, respectively (Fig. 1, A and B). This decrease in L_{exp} is comparable to the behavior observed in hexanediol (15) and indicates that the cNup153 molecules have transformed from a brush-like into

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