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Janus faced: The co-evolution of war and peace in the human species

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Abstract

The human species presents a paradox. No other species possesses the propensity to carry out coalitionary lethal attacks on adult conspecifics coupled with the inclination to establish peaceful relations with genetically unrelated groups. What explains this seemingly contradictory feature? Existing perspectives, the “deep roots” and “shallow roots” of war theses, fail to capture the plasticity of human intergroup behaviors, spanning from peaceful cooperation to warfare. By contrast, this article argues that peace and war have both deep roots, and they co-evolved through an incremental process over several million years. On the one hand, humans inherited the propensity for coalitionary lethal violence from their chimpanzee-like ancestor. Specifically, having first inherited the skills to engage in cooperative hunting, they gradually repurposed such capacity to execute coalitionary killings of adult conspecifics and subsequently enhanced it through technological innovations like the use of weapons. On the other hand, they underwent a process of cumulative cultural evolution and, subsequently, of self-domestication which led to heightened cooperative communication and increased prosocial behavior within and between groups. The combination of these two biocultural evolutionary processes—coupled with feedback loop effects between self-domestication and Pleistocene environmental variability—considerably broadened the human intergroup behavioral repertoire, thereby producing the distinctive combination of conflictual and peaceful intergroup relations that characterizes our species. To substantiate this argument, the article synthesizes and integrates the findings from a variety of disciplines, leveraging evidence from evolutionary anthropology, primatology, archeology, paleogenetics, and paleo-climatology.

KEYWORDS

cumulative cultural evolution, peace, self-domestication, War

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1 | INTRODUCTION

The human species is characterized by a seeming paradox. On the one hand, it exhibits considerable war-proneness, recurrently engaging in intergroup conflict, a relatively rare behavior among animals.¹ Although violence is a recurrent feature in the natural world,² lethal violence against members of the same species mostly occurs in dyadic interactions (i.e., between two individuals).³ Alternatively, it takes the form of infanticides, which are found in more than 100 species of mammals.³ Coalitionary killings of adult conspecifics, by contrast, are much less common, limited to only very few species among social insects, social carnivores (e.g., lions, gray wolves, spotted hyenas, African wild dogs, cheetahs), and a few primates such as chimpanzees, crested macaques, capuchin monkeys, and humans.⁴ And, among them, the magnitude of destructiveness of human warfare—especially in modern times—is unparalleled. On the other hand, the scale and range of human cooperative activities exceed those of any other species,⁵ both within groups and between groups—a feature referred to as human “ultra-sociality” or “hyper-prosociality.”^{2,5-7} The scope of human intergroup cooperation is evidenced by the wide variety of diplomatic practices that have been developed, across cultures, to promote peaceful intergroup cooperation, such as the trade of goods and gifts, alliances (including through marriages), truces, and diplomatic practices aimed at resolving conflicts through negotiation⁸⁻¹² (see Box 1). Such positive-sum relationships between groups of conspecifics are extraordinarily rare among animals.^{13,14} In most species, interactions within the group tend to be cooperative, but interactions between groups are primarily competitive or conflictual.^{14,15} A very few species of mammals (e.g., bonobos and dolphins) and certain ants engage in intergroup cooperation.^{13,16,17} But human cooperation is deemed unique among animals due to its expansive scale and complexity, its altruistic qualities, and its prevalence among large groups of individuals, including strangers and, as such, is an evolutionary puzzle.¹⁸⁻²⁰ In short, the human species is Janus-faced^{21,22}; it displays a paradoxical combination of war-proneness and of peaceful, cooperative interactions between groups unseen in other species, and which may be labeled the “human intergroup behavioral paradox.”^{23,24} No other species combines the propensity to conduct coalitionary lethal attacks against conspecifics with the inclination to extensively cooperate and engage in peaceful relations with genetically unrelated groups. What explains this seemingly contradictory feature of the human species?

The existing literature has so far struggled to fully address this question because it remains entrenched around two drastically opposing and apparently irreconcilable views. According to one view, also referred to as Hobbesian or “long chronology,” war has deep roots in the genus *Homo*.²⁹⁻³⁹ War is an evolved adaptation derived from natural selection that humans inherited from their common ancestor with chimpanzees, from which they split approximately seven million years ago. While recognizing that humans possess the ability to engage in peaceful intergroup cooperation, this perspective primarily highlights the inclination for conflict between human groups as an evolutionary adaptation. Accordingly, from this viewpoint, intergroup violence existed throughout the entire Pleistocene, before the advent of agricultural societies, and characterized nomadic as well as sedentary hunter-gatherers. Conversely, the position at the opposite side of the spectrum considers that the

human species shares with other mammals an evolved adaptation for peaceful encounters and for restraining conflict. This position is variably referred to as Rousseauian, “shallow roots,” or short chronology of war.^{9,10,40-47} It stresses the propensity of humans to develop peaceful intergroup relations, nonviolent diplomatic practices and “peace systems,” namely clusters of neighboring societies that do not make war with each other.^{44,48} Peaceful intergroup relations are deemed to be ancestral in the human species whereas, by contrast, war has shallow roots: in the arc of *Homo sapiens*’ evolution (approximately 300,000 years), it is a relatively recent cultural invention that resulted from the rise in social complexity prompted by the Neolithic (agricultural) revolution around 10,000–12,000 years ago and the emergence of sedentary, hierarchical, and densely populated agricultural societies.

But such dichotomy is misleading. The behavioral repertoire of the human species encompasses a continuum from cooperation, to competition to warfare, with very significant cross-cultural variability. An exclusive emphasis on the deep roots of war cannot make sense of the widespread use of peaceful diplomatic practices and of mechanisms for conflict management that have characterized intergroup relations across cultures.⁸⁻¹² Likewise, a one-dimensional emphasis on so-called “peace systems” and on war as a recent cultural invention overlooks the shared evolutionary origins of intergroup aggression among humans and nonhuman primates.⁴⁹ Furthermore, throughout the span of human evolution, peacemaking has largely gone hand in hand with lethal aggression.⁴⁵ As emphasized by Majolo, conflict resolution and peacemaking—two forms of intergroup cooperation—are likely to evolve in species in which the risk of aggression is high, whereas no conflict-resolution mechanisms should be expected in species where the risk of aggression is low.⁴⁹ By putting in sharp and irreconcilable contrast these two conflicting positions, such dichotomy inhibits the understanding of the diversity of the human intergroup behavioral repertoire and of its evolutionary origins.⁴⁹⁻⁵¹ While scholars have examined the interplay between in-group cooperation and out-group conflict,^{52,53} the plasticity, versatility and variability of the human intergroup behavioral repertoire—with its paradoxical mixture of violent and peaceful interactions—remain an evolutionary puzzle. The predispositions for intergroup conflict and peaceful cooperation have both deep roots, and they co-evolved. Evolution has shaped the behavioral toolkit of humans and of other species in different ways, resulting in a much more diverse repertoire of the former. The challenge is to understand when and why this Janus-faced propensity for peace and war evolved over the long span of human evolution.

The genus *Homo* emerged in Africa around 2.8 million years ago (mya).^{54,55} Over the course of most of the Pleistocene (2.6 million–11,700 years ago), humans lived as nomadic hunter-gatherers and adapted to the selective pressures of hunter-gatherer existence (On the limitations of the so-called “nomadic-egalitarian model” for Late Pleistocene hunter-gatherers, see ref.^{56,57}). It is only around 12,000 years ago in some regions, and more recently in other regions, that the Neolithic (agricultural) revolution spurred the emergence of sedentary political societies, premodern states, and empires, thereby profoundly transforming both war and diplomacy. Humans have therefore lived and interacted as nomadic hunter-gatherers for more than 99.5% of the history of the genus *Homo*.

BOX 1 A Typology of Intergroup Behavioral Repertoires

From a cross-species comparative perspective, interactions with groups of conspecifics (including both humans and nonhuman primates) can be analytically discriminated along a spectrum from intergroup conflict to tolerant encounter, to peaceful cooperation, to fusion, as illustrated in Figure 1.

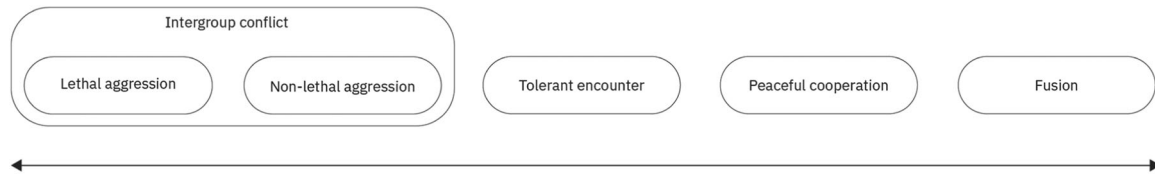


FIGURE 1 Types of interactions between groups of conspecifics.

Intergroup conflict refers to a relationship in which a coalition of members of a group seeks to inflict bodily harm on adult members of another group of conspecifics.²⁵ Coalitionary aggression can be either lethal (intergroup killing) or nonlethal, and results in costs imposed by one group upon one or more other groups, leading to a net disadvantage for at least one of the groups involved.²⁶ Coalitionary aggression against conspecifics encompasses both proactive and reactive aggression. Proactive aggression is premeditated aggression in the absence of an external stimulus, whereas reactive aggression is triggered by an external stimulus; it lacks any goal other than the immediate removal of a threat or stressor.²³

Tolerant intergroup encounters occur when individuals from different groups of conspecifics maintain visual or vocal contact without engaging in aggression towards each other.^{26,27} In these instances, the groups neither experience net costs nor receive net benefits from the interaction.²⁶

Intergroup peaceful cooperation denotes situations where members of one group willingly incur costs to provide benefits to another group, and is also referred to as *intergroup prosociality*.¹⁶ This involves the transfer of advantages from one group to one or more other groups, resulting in net benefits that are shared among multiple members of the participating groups.²⁶ This category comprises intergroup cooperation among nonhuman primates (e.g., grooming or food-sharing) as well as peaceful diplomatic exchanges and conflict management practices among humans. In this regard, diplomacy can be viewed as a subset of peaceful intergroup cooperative interaction that is characterized by communication, representation, and negotiation between groups.²⁸ Diplomatic exchanges are based upon specific social practices (representation, communication, negotiation) carried out by one or more individuals on behalf of their group. They encompass the exchange of goods, alliances, truces, conflict management and postconflict peace mechanisms, deterrence signaling and conflict avoidance, among others.

Peace refers, as suggested by Luke Glowacki, to “a condition where ongoing interactions between different social groups are marked by the absence of or infrequent occurrences of aggression and violence, alongside the expectation and presence of generally harmonious relationships not enforced with the threat of violence.”¹³ Peace is a state of interactions between individuals of different groups of conspecifics (i.e., family, kin group, clan, band, tribe, etc.) characterized by “harmonious relationships and interactions where conflicts are generally resolved and are expected to be resolved without violence.”¹³

Occasionally, one or more groups may partly or entirely merge (*fusion*), thereby forming a larger group. This fusion, which can occur either temporarily or permanently, expands the in-group to include a broader range of individuals.²⁶

Accordingly, this article examines the interplay of biological and cultural processes that have shaped the co-evolution of peaceful cooperation and conflict in intergroup relations among Pleistocene hunter-gatherers, thus laying the foundations for the subsequent diversity of diplomatic and warring practices in world history. To do so, it synthesizes and integrates the findings from a variety of disciplines, leveraging evidence from evolutionary anthropology, primatology, archeology, paleo-genetics, and paleo-climatology. Contrary to the assertions of the “deep roots” and the “shallow roots” theses, it will be argued that peace and war have both deep roots in the human species, and that they co-evolved through an incremental, stepped trajectory

over several million years rather than emerging abruptly.^{49,50,58,59} On the one hand, humans inherited the propensity for coalitionary violence from their chimpanzee-like ancestor. Specifically, having first inherited the skills to engage in cooperative hunting, they gradually repurposed such capacity to execute coalitionary killings of adult conspecifics and subsequently enhanced it through technological innovations like the use of weapons. On the other hand, they underwent a process of cumulative cultural evolution and, subsequently, of self-domestication which led to heightened cooperative communication and increased prosocial behavior within and between groups. The combination of these two biocultural evolutionary processes—coupled with feedback

loop effects between self-domestication and Pleistocene environmental variability—considerably broadened the human intergroup behavioral repertoire, thereby producing the distinctive combination of conflictual and peaceful intergroup relations that characterizes our species.

2 | WAR AND PEACE IN THE HUMAN SPECIES: A STEPPED TRAJECTORY

Why and when did the contradictory propensities for intergroup conflict and peaceful cooperation (prosociality) evolve in the *Homo* lineage, producing the distinctively human behavioral repertoire? Contrary to the claims of the “deep roots” and the “shallow roots” of war theses, both intergroup conflict and peaceful cooperation have deep roots in the human species, and they co-evolved in an incremental trajectory over millions of years (see Figure 2).

2.1 | The deep roots of proactive aggression: From cooperative hunting to war

The capacity for intergroup conflict did not develop abruptly but instead appeared gradually over several million years. In particular, the propensity for proactive coalitionary lethal aggression, inherited from the chimpanzee-like common ancestor of humans, bonobos, and

chimpanzees (LCA_{C-H}, see Box 2), was initially repurposed from cooperative hunting to targeting conspecifics and subsequently further developed through innovations like the use of weapons.

Initially, over the past 55 million years, ancestral primates focused on individual defense and aggression, protecting themselves from predators and competing for resources and mating opportunities.⁶⁰ Subsequently, the chimpanzee-like LCA_{C-H} (Box 2), from which humans split around 7 million years ago, developed the capacity to engage in cooperative hunting of small prey.^{4,24,58,60,62,63} Based upon a detailed comparison of hunting practices among extant chimpanzees and hunter-gatherers, one study inferred that the LCA_{C-H} hunted mostly small prey, often hunted in groups, occasionally appropriated carcasses from other predators (i.e., scavenging), and shared meat with social partners.⁶⁴ Since these skills could have been leveraged against members of the same species, the LCA_{C-H} likely evolved the ability for within-species coalitionary killings when it became advantageous to do so, cooperating in groups to attack individuals from rival groups.⁶⁰ As Wrangham puts it, once “our ancestors became good hunters, they could have killed strangers” since “hunting is a transferrable skill.”²⁴ He argues that the capacity for targeted coalitionary killing of conspecifics likely originated from pre-existing adaptations that enabled the LCA_{C-H} to engage in cooperative hunting and that have been repurposed for killing conspecifics (These preadaptations included robust, cooperative in-group social bonds, capabilities for coalitionary aggression, and the use of vocal signals to enhance behavioral coordination²³). In this regard, the capacity to kill conspecifics may be regarded as an exaptation,

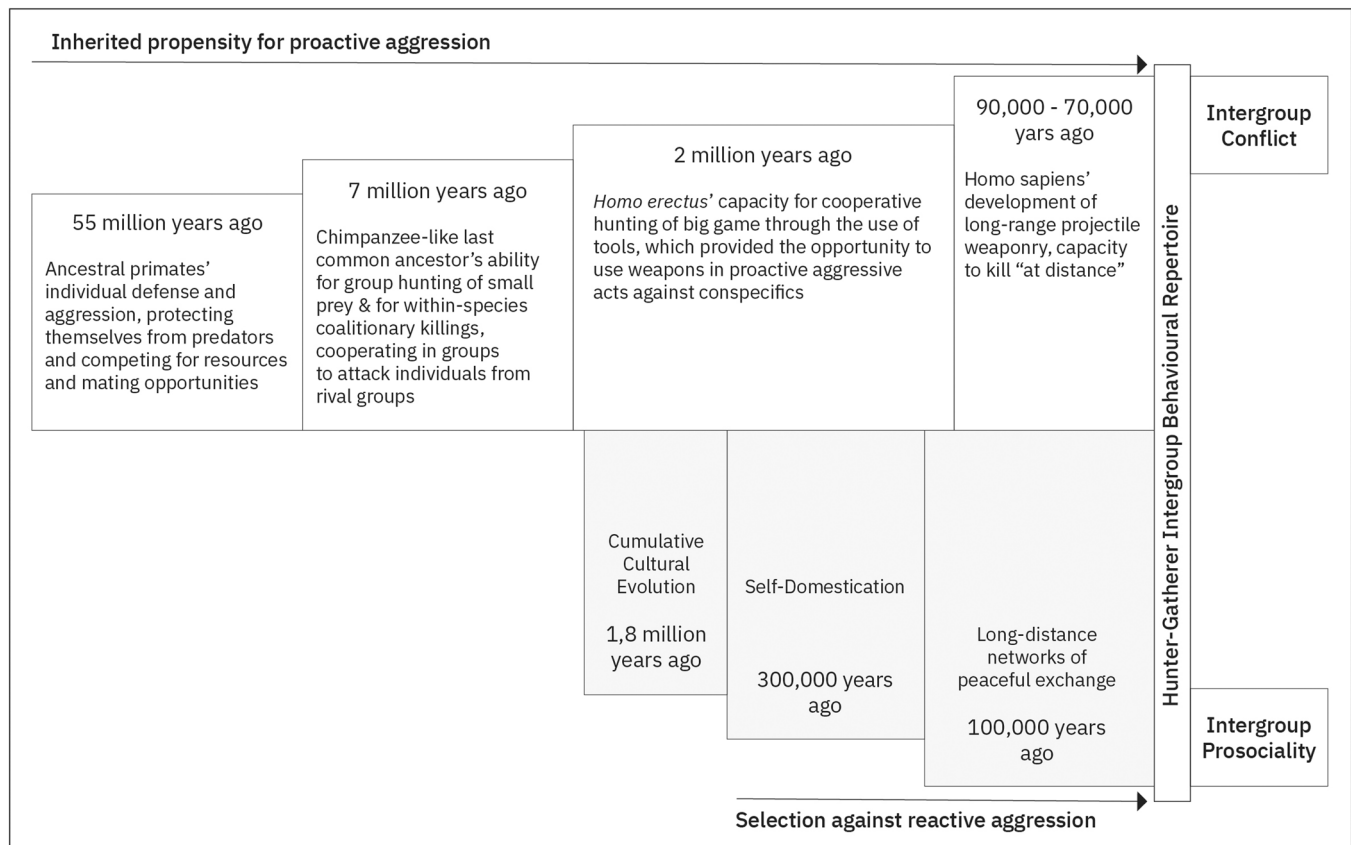


FIGURE 2 The “stepped trajectory” of war and peace. Source: Author's chart adapted and revised based upon Smith⁶⁰; and upon information retrieved from Wrangham,²⁴ Henrich,⁶¹ and Glowacki.¹³

BOX 2. The chimpanzee-like last common ancestor

Utilizing various lines of evidence, including morphology, behavior, morality, language, technology, cultural evolution, and cognitive abilities, scholars have sought to reconstruct the physical and behavioral traits of the last common ancestor (LCA_{C-H}) of humans and of their closest living relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*).

Uncertainties persist due to limited reliable fossil evidence, which has led to three main hypotheses.⁶⁴ The “Bonobo-Like Hypothesis” proposes that the LCA_{C-H} most closely resembled bonobos.^{65,66} The “Mosaic Hypothesis” suggests that no living ape is more representative than others of the LCA_{C-H}, and the traits of the LCA_{C-H} formed a mosaic of those found among bonobos and chimpanzees.^{67–69} Finally, the “Chimpanzee-Like Hypothesis” posits that the LCA_{C-H} most closely resembled chimpanzees.^{70,71}

In a collective scholarly work titled *Chimpanzees and Human Evolution*, edited by Muller, Wrangham, and Pilbeam, more than 30 scholars provided substantial evidence in support of a chimpanzee-like LCA_{C-H}.⁷² Using gorillas as a phylogenetic out-group (the species outside the group of interest when constructing an evolutionary tree), they argued that the common ancestor of chimpanzees, bonobos, and humans (phylogenetic in-group) was more chimpanzee-like than bonobo-like. First, detailed measurements of skeletal growth indicate that gorillas and chimpanzees are morphologically extremely similar and that gorillas are essentially overgrown chimpanzees.⁶⁴ Yet, contemporary genetic evidence definitively establishes humans, rather than gorillas, as the closest living non-*Pan* relatives to chimpanzees.⁷³ Fossil records further confirm that early hominins exhibited a body size akin to present-day female *Pan*, not gorillas.^{74,75} This has led to the interpretation that both *Pan* and *Gorilla* underwent minimal changes over the past 10 million years.^{74,75} Pilbeam and Lieberman conclude that both comparative data from extant species and fossil-based lines of evidence, when viewed in their phylogenetic context, indicate that the last common ancestor was morphologically similar to chimpanzees and gorillas, but resembling chimpanzees in size more than gorillas—thus supporting the idea of a chimpanzee-like LCA_{C-H}.⁶⁴

Moreover, Hare and Wrangham argue that the differences between bonobos and chimpanzees, which resemble those frequently observed in various domesticated animals compared to their wild ancestors, emerged as a result of a selection against reactive aggression and for prosociality, a phenomenon referred to as “self-domestication.”^{71,76} The morphological, anatomical, behavioral, and cognitive differences between the two species show that bonobos exhibit a juvenilized version of chimpanzee traits which resulted from a process of self-domestication. And the absence of evidence for juvenilized skeletal traits in the hominin fossil record before *Homo erectus* indicates that the bonobo condition is not ancestral, and that any shared traits with humans likely result from evolutionary convergence.⁷⁴

Accordingly, there are good reasons to treat chimpanzees as being closer to the ancestral state of *Pan* and the last common ancestor, whereas bonobos, just like gorillas, are “behaviorally and morphologically derived from a more chimpanzee-like ancestor.”⁷⁴

a trait that originally evolved for a specific function (hunting) and was subsequently repurposed for a different function.

In the past two million years, *Homo erectus* then developed the capacity for cooperatively hunting big game through the use of tools which provided the opportunity to use weapons in proactive aggressive acts and thus enhance its capacity for coalitionary killing.⁶⁰ Groups who collaborated to kill large prey using specialized tools gained a distinct advantage, especially if these innovations could be employed in raiding behaviors against conspecifics.⁶⁰

The process whereby hominins became cooperative hunters employing tools to kill large prey was itself a gradual one. Early hominins, like *Australopithecus*, initially relied on a largely vegetarian diet, with evidence suggesting plant-based subsistence from about 5.8 to 1.4 million years ago,⁷⁷ with meat representing only 1%–5% of their total diet (comparable to that of chimpanzees).⁷⁸ Despite early signs of butchery in the archeological record, the diet of hominins was not predominantly meat before 2 million years ago.⁷⁹ Two significant dietary shifts occurred over time. The first involved occasional and opportunistic consumption of

edible tissues from larger animals, supported by fossil evidence dating back to 3.4 million years ago.⁸⁰ The second shift, toward more regular consumption of such tissues, is first evidenced around 2 million years ago,⁸¹ although this claim has been disputed by contending that the best evidence for hominin butchery is instead ~2.6 million years old.^{79,82} Scholars still debate whether early hominins obtained meat through hunting/aggressive scavenging or passive scavenging after large carnivores had finished their meals.^{79,80,83} The origins of deliberate, organized hunting are still archeologically unknown, also because direct evidence of early hominins actively hunting large mammals in the Paleolithic is scarce.^{77,84} The study of ungulate prey from the 1.8 million-year-old FLK Zinj site at Olduvai Gorge, in Tanzania, has shown that early *Homo* was an ambush predator, possibly using wooden spears.^{85–87} The repeated use of a site at Ologesailie, Kenya, between 1.2 and 0.5 million years ago similarly suggests evidence of ambush hunting by *Homo erectus* around one million years ago.⁸⁸ This site was strategically chosen due to its narrow travel routes, making it easier to capture animal prey, thus implying a significant level of cooperation among early humans.⁴ Strong

evidence of hunting large deer and bovids by individuals in a residential camp dates back to about 800,000 years ago at Gesher Benot Ya'aqov.⁸⁹ Indirect evidence of hunting may also come from split animal bones, bones with cutmarks, or stone tools with wear traces left by meat cutting, but such evidence could result either from human hunting or from scavenging, and is thus inconclusive.⁸⁴ It has nonetheless been argued that a good case can be made for hunting at two early sites, at Gran Dolina (Spain, 860,000–780,000 years ago) and Boxgrove (England, 500,000 years ago).⁹⁰ The Qesem Cave in Israel also provides zooarcheological evidence of cooperative hunting, focused on large game, and food sharing in a mobile camp approximately 400,000–200,000 years ago.⁹¹

Before the development of projectile weapons, hunting weapons consisted of thrusting spears. Wooden spears found near the remains of large mammals, in various states of preservation, provide the most compelling evidence of organized hunting activities. A wooden spear found in Clacton (England, 427,000 years ago), along with a wooden spear and hunting implements discovered in Schöningen (Germany, 330,000 years ago), represent the earliest known archeological indications of hunting weapons.^{92–94} But it is mostly with *Homo sapiens*, in the last 300,000 years, that clear evidence of preplanned, cooperative hunting has been found. This is apparent in the use of projectile points, the capture of animals through apparent snare techniques, and hunting from elevated positions.²⁴ Evidence indicates that long-range projectile weaponry, likely in the form of darts delivered by spear throwers which can be used for hunting but also to kill conspecifics emerged in Africa ~90,000–70,000 years ago—if not earlier⁹⁵—and were part of the toolkit used by *Homo sapiens* when they migrated out of Africa.^{96,97}

The earliest instances of intraspecific human violence in the bioarcheological record, albeit fragmentary, appear to align with the timeline outlined above (although it is often hard to distinguish in the Pleistocene fossil and archeological record between evidence of interpersonal violence and of intergroup conflict, e.g., cranial fractures or embedded projectile points).⁹⁸ The oldest evidence of intraspecific human violence in Europe dates back to the first appearance of *Homo erectus* out of Africa, as demonstrated by healed cranial lesions at Dmanisi, Georgia, around 1.77 million years ago, possibly due to interpersonal violence.⁹⁹ At the Krapina site in Croatia, out of the skeletal remains of at least 23 Neanderthals (dating back ~130,000 years ago), four exhibit signs of antemortem blunt force trauma, one shows evidence of partially healed severe head trauma, and three upper limb and torso fragments show trauma-related pathologies.¹⁰⁰ Similarly, a forensic study at the Sima de los Huesos site in Spain, dated around 430,000 years ago, identified perimortem traumas in eight specimens (likely *Homo heidelbergensis*, although some scholars suggest that they may be Neanderthals), with conclusive evidence of interpersonal violence in one and features consistent with intentional blows in two others.¹⁰¹ Early violence among *Homo sapiens* in Europe is evidenced by the Cioclovina calvaria in Romania, dating to approximately 33,000 years ago, displaying clear signs of blunt force trauma, thus demonstrating that “the behavioral repertoire of the earliest modern Europeans also comprised violent inter-personal interactions.”¹⁰²

In the Middle East, the earliest traumatic injuries attributable to interpersonal violence among *Homo sapiens* are found in present-day Israel, at the Skhul site (a child, 120,000–90,000 years ago) and at

Qafzeh (an adult and a child, 100,000–90,000 years ago).¹⁰³ Moreover, at Shanidar in Iraqi Kurdistan, one Neanderthal individual (Shanidar 1, dated 35,000–50,000 years ago) exhibits a range of healed injuries including a frontal trauma consistent with a right-handed attacker striking with a blunt object.¹⁰³ A clearly documented example of interpersonal violence is the Shanidar 3 Neanderthal specimen (~46,000–50,000 years ago) which displays a wound in a rib caused by the penetration of a sharp object.¹⁰⁴ According to a detailed study of Shanidar 3, the position, angulation, and morphology of the lesion suggest that it was most likely inflicted “by a low-mass, low-kinetic energy projectile weapon.”¹⁰⁴ Given that projectile weapons were part of the toolkit of *Homo sapiens* as they migrated out of Africa but not of Neanderthals, it has been suggested that Shanidar 3 may demonstrate interspecific violence by *Homo sapiens* against Neanderthals.^{60,104}

The oldest documented instance of interpersonal violence in Africa is found among *Homo sapiens* around 23,500–19,300 years ago at Wadi Kubbaniya, in the Nile Valley, where a young adult male displays healed forearm parry fracture and embedded projectiles.¹⁰⁵ Additionally, the Qadan graveyard at Jebel Sahaba in Sudan, dating between 13,400 and 18,600 years old, reveals 23 out of 61 bodies with signs of violent deaths, although debates persist over whether these deaths resulted from large-scale raids or isolated instances of violence over time.^{60,106} In Eastern Africa, the site of Nataruk, located west of Lake Turkana in Kenya and dating to approximately 9,500–10,500 years ago, provides compelling evidence of intergroup violence among hunter-gatherers, with the discovery of 12 partially preserved bodies, 10 of which exhibit clear signs of death due to sharp and blunt force trauma inflicted by arrows and clubs.^{107,108}

All in all, the bioarcheological record brings to light the deep roots of intraspecific human violence, although the extent to which it took the form of in-group or intergroup violence is often left unanswered by the available evidence.

But what were the motivations for early *Homo* to kill conspecifics? Over time, the benefits gained from aggression extended beyond immediate biologically driven resource gains to encompass also cultural benefits. On the one hand, the benefits reaped by aggression for humans were initially, at least in part, akin to those observed in chimpanzees, involving increased territory, enhanced access to resources, and the ability to repel competitors for mates.^{109–113} In this regard, intergroup conflict among early hominins yielded direct benefits comparable to patterns seen in chimpanzees, with successful groups securing expanded territory encompassing valuable resources (such as food or mates).^{109–114} On the other hand, in contrast to nonhuman primates, early *Homo* likely gained a broader array of benefits, including the acquisition of captives, transportable goods, and within-group cultural rewards.^{32,33,113,115,116} The introduction of intangible cultural rewards, such as status or prestige, created additional incentives for individuals participating in intergroup aggression.¹¹³ The “cultural rewards war-risk hypothesis,” in particular, posits that “the opportunity for warriors to benefit more from their participation in warfare is associated with greater conflict intensity.”¹¹⁵ Glowacki and Wrangham found a positive correlation between the mortality rate in war and the total number of benefits that hunter-gatherer warriors might receive from participating in war (Cultural Benefits for Warriors, CBW_T), which include immaterial rewards such as increased status, more allies, or

earlier age at marriage, among others.¹¹⁵ While pinpointing the exact emergence of cultural benefits like status and prestige is challenging, it has been suggested that these features likely originated with the development of group living and advanced social learning capacities, a trait potentially present in *Homo erectus*.^{113,115} In other words, cultural benefits from aggression likely coincided with the emergence of cumulative culture.

2.2 | The deep roots of peaceful intergroup relations: Cumulative culture, self-domestication, and prosociality

While proactive coalitionary aggression is a phylogenetically inherited trait, the propensity for peaceful intergroup relations (between-group prosociality) is a derived trait, i.e. an evolutionary innovation that evolved in the human species after the divergence of the *Homo* and *Pan* (chimpanzees and bonobos) lineages. The capacity for peaceful intergroup relations is a trait that humans have in common with bonobos, but not chimpanzees, which do not engage in intergroup cooperation. Furthermore, the scope and range of intergroup cooperative activities among human groups is vastly wider than among bonobos.¹¹⁷ Since, as detailed in Box 2, the LCA_{C-H} was most probably chimpanzee-like, the propensity for peaceful intergroup relations is thus likely a derived trait in the human species.^{118–120} As Hames puts it, “war is a chimpanzee invention and peace is a human invention.”^{118,119} When and how did the propensity for between-group prosociality emerge? Similarly to how human intergroup conflict developed in a step-wise fashion, peaceful intergroup relations too evolved gradually and cumulatively over millions of years.

A first critical threshold in the trajectory towards intergroup prosociality was, as Joseph Henrich persuasively argued, crossing the “Rubicon” of cumulative cultural evolution around 1.8 million years ago.⁶¹ Culture can be defined as “group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted information.”¹²¹ Cultural learning has been shown to be present in many species (e.g., great apes, capuchin monkeys, whales, dolphins, wild birds) that transfer skills through social learning, resulting in stable differences between subpopulations.^{61,122,123} Yet, the genus *Homo* is deemed to be unique in its capacity for cumulative cultural evolution, that is, the process whereby cultural traits are improved (in terms of complexity or efficiency) over successive generations to eventually result in products that could not have been invented by a single individual alone.¹²² The transmission of these cultural traits can occur through emulation from biological parents (vertical transmission), from peers (horizontal transmission) and/or from other members of older generations (oblique transmission). Cumulative cultural evolution is locally adaptive: culturally transmitted information accumulates over generations such that tools and know-how become increasingly better suited to the local environments, thereby producing enormous cultural diversity. This “ratcheting up” in the complexity of locally adaptive cultural traits significantly widened and diversified the intergroup behavioral repertoire of early *Homo*.¹²⁴

Specifically, cumulative cultural evolution greatly influenced both intergroup conflict and peaceful cooperation. On the one hand, cumulative cultural evolution first introduced and over time broadened the cultural benefits arising from intergroup conflict, as previously discussed. On the other hand, cumulative culture has facilitated teaching within and across generations while enabling the evolution and sophistication of language, thus prompting larger-scale cooperation. (The timing of the emergence of language remains a hotly debated issue in the scholarly literature; for diverging views on the origins of proto-language and language among saltationists, gradualists and proponents of the multicomponent model, see among others^{125–127}). Laland suggests that (proto)language initially developed to improve the efficiency and scope of teaching.^{128,129} Over the past 2 million years, early *Homo* developed increasingly complex cultural innovations (e.g., tools and foraging techniques) such that their communication required constant updating and elaboration of signals and meanings. This suggests that (proto)language might have co-evolved with cultural complexity to aid in the enhancement and transmission of skills among early *Homo*.¹²⁸ Language, in turn, has played a pivotal role in expanding group sizes and in facilitating interactions across group boundaries. Over time, cultural practices that rely upon language such as the extension of kinship to affinal ties, marital arrangements between and across groups, long-distance networks of exchange as well as peacemaking and conflict resolution practices have gradually contributed to the growth of human groups and the establishment of peaceful relationships between them.^{113,130–132} As Laland puts it, “the advent of teaching through language was a game changer” because “it hugely enhanced the scale and mechanisms of cooperation.”¹²⁸

When did cumulative culture first emerge? Given that chimpanzees and other primates lack cumulative culture, it is reasonable to assume that the LCA_{C-H} also did not possess cumulative culture and was no more culturally advanced than modern chimpanzees.⁶¹ The last common ancestor had not yet entered the realm of cumulative cultural evolution. Around 3.4 million years ago, in Ethiopia, hominins used stone tools for food processing, such as cutting and scraping the meat off ungulates, reflecting increased social learning capabilities.⁶¹ By 2.6 million years ago, the so-called Oldowan tools emerged, crafted and shaped for diverse tasks such as cutting meat, breaking bones, scraping hides, and slicing through tough materials.⁶¹ By 1.8 million years ago, the transition to *Homo erectus* marked a crucial acceleration in cultural evolution, with larger brains, more sophisticated stone tools, and evidence suggesting increased dependence on food processing.⁶¹ It was around this moment, 1.8 million years ago, according to Henrich, that the *Homo* lineage first crossed the evolutionary threshold of cumulative cultural evolution. *Homo erectus* gained control over fire and engaged in cooking, with indications dating back to potentially 1.5 million years ago and more convincing evidence around 800,000 years ago.^{61,133,134} In Africa, *Homo erectus* coexisted with distinctive large stone tools, different from the Oldowan tools, requiring specific materials extracted from quarries.⁶¹ This period also witnessed the development of knowledge related to animal behavior, tracking, and the creation of water containers,

potentially enabling *Homo erectus* to participate in long-distance persistence hunting or scavenging.⁶¹ And, by around 850,000 years ago, *Homo erectus* demonstrated increased tool sophistication by thinning large cutting tools and achieving greater symmetry.⁶¹ The *Homo* lineage had now embarked on the path of cumulative cultural evolution and teaching through (proto)language, thereby widening the scope of intergroup cooperation.

The second critical threshold was crossed when, slightly before 300,000 years ago, the human species underwent a process of selection against reactive aggression (or self-domestication) which resulted in improved cooperative communication and greater prosociality, both within and between groups. This self-domestication process, as explained below, was likely spurred by the advent of language (or proto-language) and thus at least partly enabled by cumulative cultural evolution.

As shown by Hare and Wrangham, various lines of evidence—*anatomical, developmental, cognitive-behavioral, neurological, and genetic*—indicate a reduction in reactive aggression and the emergence of domestication syndrome traits, including greater prosociality.^{135–137} For one, self-domestication brought about a range of anatomical changes in *Homo sapiens*. Anatomical transformations in human skulls also found in domesticated animal species are evident from the Middle Pleistocene (after 200,000 years ago), marked by a 40% reduction in brow ridge projection, shorter faces, and reduced sexual dimorphism, combinedly referred to as gracilisation.^{136–138} This trend has continued, resulting in modern hunter-gatherers and agriculturalists having even more juvenile facial appearances than their Late Pleistocene ancestors.¹³⁷ In short, “gracilisation tendencies similar to those found in domestication are found throughout the evolution of *Homo sapiens*.”¹³⁷ Moreover, finger measurements, particularly the ratio of the length of the index finger to that of ring finger (or 2D:4D ratio), similarly reveal that Middle Pleistocene humans had a lower, more “masculinized” ratio compared to modern humans, which is associated with a greater degree of risk taking and potential for aggression (a lower 2D:4D ratio is typically observed in men as compared to women, and is therefore typically referred to as “masculinized”),^{136,137} Neanderthals exhibited more “masculine” 2D:4D ratio, indicating that the more “feminized” 2D:4D observed in modern humans emerged relatively late, coinciding with the emergence of more gracilized facial features.^{136,137} Likewise, the presence of white sclerae in human eyes, unique among primates, in conjunction with colorful irises enabled increased visibility during eye contact, underscoring a transition from concealing to showcasing one's eyes—reflecting the greater cooperative communication and prosociality prompted by the process of self-domestication.^{71,137} The question of the brain size remains a vexing issue in the debates on self-domestication. Given that the reduction in brain size is a common feature of domesticated animals, the trend of growing brain size during most of human evolution would appear to contradict the self-domestication hypothesis.¹³⁹ Yet, several studies have shown that, after several million years of steady growth, the human brain size declined over the past 50,000 by 5.415% (other studies provide a slightly different timeline,

identifying a more recent reduction in brain size, around 10,000 years ago),^{140–142} coupled with a shift to more globular skulls compared to Neanderthals.^{137,143} Wrangham further emphasizes that modern human skulls—and, by inference, their brains—exhibit paedomorphic features compared to Neanderthals in that, when *Homo sapiens* skulls cease growing, their shape resembles that of a Neanderthal skull in its penultimate of growth, thus aligning with aspects of the domestication syndrome.²⁴

At developmental level, a notable consequence of self-domestication is the extension of the juvenile period, known as neoteny, influencing learning environments and opportunities. The extended juvenile not only enhances learning by offering more chances for cultural exposure, imitation, and shared experiences, thus enabling the acquisition of a broader range of signals, but it is also associated with increased (allo)parenting and explicit teaching behaviors, providing direct support for the learning process.¹⁴⁴

From the cognitive and behavioral standpoint, comparisons with living domesticated animals, especially dogs and foxes, uncover similarities in traits such as low reactive aggression, high play, high tolerance, cooperative communication, and high prosociality.¹³⁶ As stressed by Wrangham, “all of these features are found in humans, suggesting that their occurrence is owed to a process of domestication similar to the evolution of dogs from wolves.”¹³⁶ Crucially, the process of self-domestication has been accompanied by greater “cooperative communication,” namely the understanding of the deliberate sharing of useful information,¹³⁵ which enabled shared intentionality, i.e. “collaborative interactions in which participants share psychological states with one another.”¹⁴⁵ This enhanced cooperation, social tolerance, playfulness, and reduced reactive aggression have resulted in more frequent and more elaborate connections with both kin and nonkin individuals, which characterize the widespread social networks of humans.¹⁴⁴

The neurological evidence for decreased reactive aggression and heightened tolerance which resulted from self-domestication includes elevated serotonin and oxytocin levels, a decline in testosterone production, socially regulated cortisol levels, and increased neurogenesis in the hippocampus.^{23,144,146} As an example, both humans and other domesticated species commonly display heightened serotonin levels, which have been demonstrated to encourage defensive behaviors rather than offensive ones in animals.^{23,144,146}

Finally, paleo-genomic data provide further insights into the self-domestication syndrome. By comparing the genomes of *Homo sapiens* with those of Neanderthals, Denisovans, and various domesticated species such as dogs, cats, horses, and cattle, a study by Theofanopoulou et al. identified 41 genes that show positive selection in both *Homo sapiens* and domesticates, but not in the other human species.¹⁴⁷ This genomic evidence provides support for the “domestication syndrome” through changes in specific signaling pathways and cellular lineages, particularly those related to the neural crest.¹⁴⁷ Alterations in genes associated with the neural crest, specifically the regulatory gene BAZ1B, resulted in modified behavior of neural crest cells in *Homo sapiens*, consistent with the anticipated outcomes of the self-domestication hypothesis.¹³⁶

Accordingly, multiple lines of evidence coalesce in supporting the hypothesis of a human self-domestication syndrome which resulted in a decreased propensity for reactive aggression and an increased propensity for cooperation and prosociality.^{23,136} With regard to its temporality, the idea that human self-domestication began around 300,000 years ago stems from the observation that the most recent phase of this self-domestication process is unique to *Homo sapiens*, with earlier Pleistocene *Homo* species lacking signs of a self-domestication syndrome, such as gracilization.¹³⁶ The absence of such changes in Neanderthals, coupled with the genetic data indicating a split between the lineages leading to Neanderthals and *Homo sapiens* around 270,000–765,000 years ago, suggests that the distinctive evolution of self-domesticated traits of *Homo sapiens* likely commenced within this timeframe.¹³⁶ Additionally, as mentioned, genetic comparisons with Neanderthals and Denisovans indicate anatomical signs of self-domestication found exclusively in *Homo sapiens* but not in these other human species, supporting the hypothesis that self-domestication in *Homo sapiens* began shortly prior 300,000 years ago.¹³⁵

What spurred this self-domestication process? The execution hypothesis, proposed by Wrangham building upon previous work by Boehm, posits that the selective pressure for self-domestication in *Homo sapiens* resulted from the ability to predictably eliminate coercive alpha males through proactive intragroup killings, facilitated by language-mediated social alliances among beta males against the alpha male.^{24,135,136,148} While chimpanzee and bonobo societies are clearly hierarchical, nomadic hunter-gatherer communities operate on an egalitarian basis, with no alpha individual. The ancestor of *Homo sapiens*, *Homo heidelbergensis*, is thought to have inhabited social communities which displayed the dominance hierarchies typical of primates living in multi-male, multi-female groups.¹³⁵ So how did the dominance hierarchies of the LCA_{C-H} and of *Homo heidelbergensis* transition into the egalitarian hunter-gatherer communities of *Homo sapiens*? This resulted from a levelling mechanism that prevented the establishment of personal dominance among adult individuals, often through capital punishment or the execution of aspiring leaders.¹¹⁸ In particular, Wrangham argues that a specific form of capital punishment among *Homo sapiens*, targeted conspiratorial killing—a “uniquely human tendency in which a coalition cooperatively chooses and kills individuals within a social community”—played a central role in controlling (and executing) coercive males.^{23,24,135,136,148} Boehm identified 48 societies of hunter-gatherers where deliberate measures were taken to confront undesirable behaviors displayed by leaders, including 11 cases of leader assassination.¹¹⁸ Such levelling mechanism through coalitionary intragroup killing of the aspiring dominant individual, a human specificity, drove selection against reactive aggression, thereby spurring the transition from dominance hierarchies to the egalitarian structure of hunter-gatherer societies, a “reversed dominance hierarchy.”^{23,24,135,136,148} This type of coalitionary killing has been enabled by language, which was key for beta-males to agree that a specific victim should be killed and to coordinate the execution. Such language-based conspiracy, centered on shared intentionality

communicated through language—that other primates lack—explains why it is not found in other primates.

In short, the emergence of (proto) language, which was partly enabled by cumulative cultural evolution, played a crucial role in shaping the selective pressures that spurred this self-domestication process and enhanced prosociality of the human species. In turn, the process of self-domestication, which is characterized by reduced reactive aggression, increased prosociality, an extended juvenile period, and enhanced playfulness—all traits that rely on cooperative communication—significantly influenced the development and sophistication of language in a positive feedback loop.^{149–151} More tolerant and prosocial individuals established stronger and denser social networks, encompassing both kin and nonkin. The increased social connections that resulted from these networks necessitated more informative and cognitively demanding language.¹⁴⁴ In turn, the development and sophistication of language further facilitated complex cooperative interactions within and between social groups.¹⁴⁹

The third and final critical threshold in the incremental development of peaceful intergroup relations was largely a consequence of the preceding two. Combinedly, cumulative cultural evolution and self-domestication prompted a major expansion in both the size and interconnectedness of human groups in the past 100,000 years ago, and thereby widened the scope of peaceful intergroup relations.

As humans became more prosocial, they gradually shifted from living in small groups to larger bands of hundreds or more.^{137,146,152} Between 300,000 and 25,000 years ago, *Homo sapiens* had estimated community sizes ranging from 120 to 150 members.¹⁵³ But cooperative communication and prosociality did not affect only group size. By enabling greater cooperation, they also triggered a major expansion in the interconnectedness of the human species, both within and between groups. Starting around 130,000 years ago in Africa and 100,000 years ago in Europe transfer distances of materials began exceeding 300 km, suggesting the emergence of extensive long-distance exchange networks among Pleistocene hunter-gatherer groups.^{154,155} By 50,000 years ago there is ample evidence of large-scale trade between Eastern and Southern Africa, as demonstrated by trade networks of ostrich eggshell beads.¹⁵⁶ While the *maximum* transfer distance had exceeded the 300 km, the European Upper Paleolithic (40,000–10,000 years ago) also exhibited a “dramatic increase,” in the words of Féblot-Augustins, in the volume of transfers exceeding 100 km.¹⁵⁴ In certain areas, the frequency and range of long-distance during the Upper Paleolithic further increased, with some materials (such as shells and fossils) moving up to 1000 km across the continent.¹⁵⁷ The overall archeological record thus suggests the initial emergence and subsequent expansion of extensive long-distance exchange networks among hunter-gatherer groups in both Africa and Europe during the Paleolithic, possibly representing the earliest archeological evidence of peaceful between-group interactions in human prehistory.

Summing up, cumulative cultural evolution and language-enabled self-domestication created interlocked feedback loops that gradually fostered enhanced prosociality, the development of long-distance

networks of exchange, and the expansion of peaceful intergroup relations. Over time, these biocultural (or gene-culture) co-evolutionary processes produced what Joseph Henrich calls autocatalytic change, whereby the outcome of a process acts as a catalyst that further catalyzes that process, intensifying and accelerating it.^{61,158} Cumulative culture has enabled the passing down of knowledge and skills within and across generations and facilitated the development of (proto)language, which may have initially evolved to improve teaching efficiency. Language, in turn, enhanced cooperative communication and enabled shared intentionality, thereby playing a pivotal role in the coalitionary killing of aspiring dominant individuals and the selection against reactive aggression (or self-domestication). As humans became more prosocial through self-domestication, they established increasingly large social networks, fostering the exchange of ideas, goods, and information over long distances. This expansion of social networks further fueled the development of language and cumulative culture, creating a positive feedback loop that widened and diversified peaceful intergroup cooperative relations.

Additionally, an overarching selective pressure that favored intergroup peaceful cooperation throughout the Pleistocene was environmental variability. Approximately 3 million years ago, Earth's climate became increasingly variable, with a further intensification of climatic instability during the mid- to late-Pleistocene.^{61,159} The pace of wet-dry fluctuations in tropical Africa followed approximately 20,000-year cycles of orbital precession (changes in the orientation of Earth's rotational axis), while variations in Earth's eccentricity (the degree of deviation of its elliptical orbit from a perfect circle) on cycles of about 100,000 and 413,000 years influenced the overall pattern of seasonal precipitation intensity and duration.¹⁶⁰ These climate fluctuations were characterized by shifts in forests, lakes, savannahs, and woodlands, and coincided with a general trend toward cooler and dryer conditions globally.⁶¹ This climate variability likely acted as a significant driver of hominin evolution and further intensified the selection pressures for social learning and intergroup prosociality spurred by the process of self-domestication of *Homo sapiens*.

The "variability selection hypothesis," introduced by Potts and collaborators, posits that environmental variability has significantly shaped genetic and cultural adaptations in hominins and other organisms.¹⁶¹ It suggests that versatile phenotypes—and their underlying genetic basis—have been selected for during periods of heightened environmental variability, leading to the evolution of traits that enhance adaptability through physiological, behavioral, and ecological plasticity, thus enabling hominins to thrive in a variety of different habitats.¹⁶¹ *Homo erectus* evolved during a period of growing global climate variability, while *Homo sapiens* appeared amid the most intense fluctuations.¹⁶¹

This Pleistocene environmental variability acted as an overarching selective pressure that favored intergroup peaceful cooperation. It has been argued that intergroup cooperation and long-distance exchange proved crucial for accessing nonlocal resources and thereby dampen the adverse consequences of environmental variability and resource unpredictability.^{162,163} Over the past

300,000 years—and even more so in the last 130,000 years—*Homo sapiens* developed ever-expanding networks of exchange in multiple continents (as discussed above), which likely served as buffering mechanisms in the face of climatic instability. Buffering refers to practices that seek to lessen the impact of environmental variability by dampening its effects. As Migliano and Vinicius put it, intergroup exchange "over long territories buffers against resource unpredictability, seasonality and environmental depletion."¹⁶⁴ Simulation modeling has indeed shown that intergroup tolerance and cooperation, involving the sharing or exchange of resources, significantly enhance population survival under conditions of environmental variability.¹⁶⁵ Populations engaging in resource-sharing are more likely to thrive, leading to increased population size and a higher likelihood of survival compared to those that do not engage in resource sharing.¹⁶⁵ Spikins and colleagues therefore conclude that the periods of increasing environmental variability between 300,000 and 30,000 years ago "may have provided the conditions in which elevated selection pressures on intergroup social tolerance might have emerged, leading to the passing of a threshold point beyond which intergroup collaboration became a normal stable state," a transformation in social behavior associated with "self-domestication."¹⁶⁵ In short, environmental variability at a time when *Homo sapiens* was undergoing a process of self-domestication process likely intensified selective pressures favoring the behavioral plasticity of *Homo sapiens* and its propensity to engage in peaceful intergroup exchange.

3 | CONCLUSION

Contrary to the claims of the "deep roots" and the "shallow roots" theses, both war and peace have deep roots and they did not emerge suddenly, but rather co-evolved through a gradual, stepped trajectory over million years. On the one hand, while humans inherited the inclination for proactive aggression from their chimpanzee-like ancestor, the acquisition of the specific ability to carry out preplanned coalitionary killings emerged gradually through incremental steps, dependent on a combination of biological propensities, advancements in cognitive capacities, and technological innovations, including the evolution of cooperative hunting and the development of weapons. On the other hand, the propensity for peaceful intergroup relations similarly evolved gradually and cumulatively over millions of years after the split from the *Pan* lineage. Having first developed the capacity for cumulative cultural evolution, a process of self-domestication then led to heightened cooperative communication and increased prosocial behavior, both within and between groups. This, in turn, drove a significant increase in both the scale and interconnections of human groups, thereby enabling the expansion of their networks of peaceful exchange, a trait that proved crucial to access nonlocal resources and thus cope with Pleistocene environmental variability. This two-pronged gene-culture co-evolutionary process—and its mutually reinforcing feedback loops—largely explains the idiosyncratic human

intergroup behavioral repertoire and the distinctive blend of war and peace that characterizes the human species. It laid the foundation upon which sedentary civilizations, city-states, and empires rose and fell, and for the ways in which they conducted diplomacy and waged war. It paved the way for the continued persistence of both war and peace in our species.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available.

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