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Cultural Evolution and the Deep Roots of Cooperation: A Unified Perspective

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Abstract

This essay frames the evolution of human cooperation as a two-layer process. A foundational layer, rooted in subsistence and ecological pressures, shaped cooperative dispositions unevenly, whereas an expansionary layer, rooted in conflict, political stratification, and shared infrastructure, generated large-scale, institutionalized cooperation. The first evolutionary layer unfolded over the grand arc of human evolution, reinforcing the capacity for small-scale cooperation in hunter-gatherer societies while favoring traits complementary to cooperation only in some sedentary societies. The second evolutionary layer emerged as rising population density heightened external threats, fostered coercive centralized authority, and raised the returns to public infrastructure. In environments where cooperative traits had already evolved, warfare, extraction, and infrastructure provision reinforced these predispositions, scaling them into durable collective institutions. Yet in regions where such cultural foundations were absent, large-scale collective action was more challenging, and conflict was often destabilizing, magnifying division and political fragility. Recognizing the profound global heterogeneity in this foundational layer of cooperative behavior is essential for identifying the origins of large-scale cooperation and the conditions under which conflict enhanced this capacity.

Keywords: Cultural Evolution, Unified Growth Theory, Future-oriented mindset, Cooperation, Malthusian epoch, The Journey of Humanity

JEL Classification Codes: O10, 040, Z10

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1. Introduction — Roots of Cooperation and Social Complexity

The human journey across tens of millennia has unfolded through demographic, technological, and cultural transformations, yet the widening scale of cooperation stands among the most consequential.

Human social evolution, like that of other primates, was shaped within small groups, where cooperation relied on behavioral dispositions sustained through repeated interaction, informal enforcement, reciprocity, and kin-based trust. For most of human existence, cooperation remained predominantly local in scale, often anchored in kinship networks. Yet humans inherited and further evolved a capacity for cooperation beyond kinship.[1] The emergence of sedentary communities during the Neolithic Revolution, nearly 12,000 years ago, intensified this predisposition and amplified its regional divergence, allowing cooperation to scale from villages to towns, cities, states, and empires.[2]

As population density rose, labor was organized collectively for undertakings that individuals could rarely execute in isolation. Cooperation extended far beyond the circle of kinship, as people were mobilized to construct public infrastructure, erect symbolic monuments, defend shared territory, and sustain the institutions through which shared identity was formed. These collective enterprises included irrigation systems that stabilized output across seasons, communal storage that buffered periods of scarcity, transport corridors linking settlements and markets, defensive structures providing communal security, and standing armies that supported durable social organization, and contributed to long-run stability. These activities generated growing demands for cooperation at scale.

Meeting these organizational pressures required more than ad hoc coordination; it depended on durable organizational structures. As production began to generate modest, temporary surpluses, incremental specialization emerged, giving rise to a non-food-producing class that devoted its labor to thinking rather than tilling, discerning patterns, refining techniques and generating knowledge, while also legitimizing and enforcing emerging social hierarchies.[3] Across millennia,

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[1] See, Boyd and Richerson (1985) and Sober and Wilson (1998).
[2] Galor (2022)
[3] See Diamond (1997), Ashraf and Galor (2011), and Galor (2005, 2011, 2022, 2025).

this social class advanced writing, mathematics, science, engineering, and systems of record-keeping, often facilitating extraction and social control. Kinship rules solidified into legal codes; tribal norms were transformed into formal institutions; and cooperation extended beyond the boundaries of kinship, frequently shaped by asymmetrical power relations rather than purely voluntary alignment. This expanding sphere of collective action was not merely a consequence of structural change, but a mechanism through which public infrastructure was constructed, knowledge preserved across generations, and social complexity deepened. Rising scale and density amplified this process, enabling greater institutional capacity, specialization, and societal transformation.

What evolutionary forces enabled cooperation to extend beyond the narrow boundaries of kinship? Two distinct but interacting evolutionary layers appear to have been instrumental. The first unfolded over the grand arc of human evolution under subsistence and ecological pressures, shaping inherited cooperative dispositions within and across social groups. In hunter-gatherer societies, these forces reinforced the group-level capacity for coordination through repeated interaction, informal enforcement, reciprocity, and kin-based trust. Following the Neolithic transition, as settlement and subsistence regimes diverged across environments, these ecological forces continued to act directly on cooperative predispositions, differentially selecting a broader set of traits complementary to cooperation. This process of development favored traits conducive to cooperative capacity in some sedentary societies but not in others, generating cross-societal variation in the foundations upon which large-scale cooperation could later emerge.

The second evolutionary layer emerged at the group level as rising population density intensified intergroup contact, political stratification, and infrastructure provision. These forces expanded coordination beyond local groups, encompassing not only collective mobilization for conflict but also the provision of public infrastructure, administrative organization, and the management of hierarchy. In environments where cooperative predispositions and their complementary traits were already prevalent, these pressures built on existing foundations, facilitating coordination at scale and transforming cooperative capacity into public goods, standing armies, and bureaucratic systems. Yet in regions where such cultural foundations were weaker, large-scale coordination was difficult to sustain, and conflict often proved destabilizing, magnifying division, predation, and political fragility rather than supporting durable cooperation.

Intergroup conflict and the emergence of institutions became arenas through which pre-existing cultural predispositions toward cooperation were reinforced and amplified. In regions where cooperative foundations had been more entrenched, conflict and institutional development fostered reciprocity and sustained broad-based cooperation. Yet in settings where such predispositions were weaker, effective state formation typically relied on coercive coordination within ruling coalitions, privileging military organization, predation, and warfare over cooperation in production and exchange.

Recognizing the distinct roles of these two evolutionary layers is therefore essential for understanding the historical scaling of cooperation and, in particular, for the proper framing of empirical inquiries into the impact of conflict on cooperative capacity. These interconnected layers present formidable challenges for the empirical assessment of this relationship. Since pre-existing cooperative capacity governed the onset of intergroup conflicts, including those triggered by drought, invasions, or other external shocks, conflict cannot be treated as an exogenous shock in the evolution of cooperation, as it tended to arise more frequently where barriers to collective mobilization were lower. Observed correlations between conflict and cooperation, rather than being indicative of a causal effect of conflict on cooperation, may instead capture reverse causality as well as the influence of unobserved factors that jointly foster cooperation and the likelihood of conflict. Moreover, since cooperative predispositions persist over time and current levels are correlated with their past realizations, lagged measures of conflict do not resolve these identification barriers. Assessing the impact of conflict on cooperation requires disentangling the persistence of underlying cooperative tendencies from any incremental effects attributable to the onset of conflict per se.

2. Cooperation Through Conflict and Group-Based Selection

2.1. Conflict as a Driver of Cooperation: Theoretical Framework

Human societies did not evolve in isolation. They emerged alongside neighboring communities, competing over fertile land, reliable water sources, and essential raw materials. In this environment of intergroup rivalry, survival often hinged on the ability to mobilize populations toward shared

goals, such as investing in infrastructure, fortifying defenses, and waging war. Cohesive ruling coalitions, unlike fractured ones, possessed the organizational capacity to construct fortifications, store grain, and raise armies, often relying on coercion, hierarchy, and discipline.[4] External threats frequently bound communities more tightly than the prospective gains from shared public goods.

Turchin (2025) advances a rigorous and insightful conflict-centered theory of cooperation, arguing that the rise of large-scale, hierarchical societies was driven less by material abundance than by sustained intergroup conflict. In his account, recurrent conflict selectively favored social structures capable of sustaining collective mobilization, centralized authority, and military capacity over long horizons. He links warfare and competition between polities to the emergence and persistence of sociopolitical complexity, public goods provision, and political hierarchies, and examines the empirical validity of these relationships using longitudinal historical evidence from the Seshat Global History Databank across hundreds of premodern societies.

Seen through this lens, surplus generated from public goods was not necessarily the dominant force that initially scaled human cooperation. Rather, external pressures associated with intergroup conflict rendered large-scale coordination essential for survival and endurance, often within ruling coalitions rather than across the broader population. Cohesion emerged and persisted insofar as it enhanced collective performance within these coalitions. Groups able to organize labor, invest in public infrastructure, and mobilize armies prevailed and at times absorbed or displaced less cohesive neighbors. Intergroup conflict thus acted as a selective filtering mechanism, conferring a durable edge in endurance and expansion on societies with stronger capacities for coordinated action.

This warfare-driven cultural selection theory of cooperation proposes that under persistent external threat, societies that endured were those able to coordinate collective action and translate it into effective political organization. Military success relied not only on metallurgy and cavalry but equally on cohesion and disciplined cooperation, often deliberately cultivated by ruling coalitions. Such a governing capacity, in turn, enabled the mobilization of populations for defense and territorial expansion, as well as the construction of public infrastructure and the maintenance of standing armies. It fostered the emergence of administrative systems capable of extracting and

[4] An extensive literature also examines how cooperation can be sustained through internally generated norms, monitoring, and rule-based governance, independent of external conflict (Ostrom 1990).

allocating resources for storage, irrigation, fortification, and military supply, supported by tax compliance and the steady flow of grain surpluses. Religion often reinforced this institutional structure, sanctifying hierarchy, obedience, and sacrifice, through shared beliefs, rituals, and symbols. In reinforcing these arrangements, it contributed to the formation of shared social identity, allowing systems of coordination and compliance to crystallize into enduring institutions. The resulting administrative order provided the stability that supported cities, states, and eventually empires.[5]

2.2. Historical Illustrations of Conflict-Based Cooperation

Patterns consistent with these predictions appear across ancient and pre-Columbian civilizations (Turchin, 2025). In Mesopotamia, repeated invasions and interstate rivalries fragmented existing polities, favoring those capable of restoring authority and mobilizing resources on a broader scale. In ancient China, recurrent warfare across the Yellow River plains, especially along the northern frontier with steppe societies, necessitated systematic grain storage, long-distance logistics, and organized public labor for defensive walls, canal transport, and irrigated agriculture, thereby reinforcing centralized authority. As coordination expanded from local clans to regional states, political consolidation became more durable, and periods of unification brought greater institutional stability. In the Aztec heartland of the Basin of Mexico, rivalry among city-states required pooled resources, tribute collection, and sustained military provisioning, leading to the formation of the Triple Alliance that gave rise to the Aztec Empire. Across these regions and time periods, conflict operated as a selective force that magnified the organizational advantages of collective action, where they already existed and favored polities capable of sustaining large-scale mobilization beyond kinship networks, often through coercive authority rather than broad-based popular allegiance.

2.3. Empirical Evidence and Identification Challenges

Drawing on the Seshat Databank, Turchin (2025)'s empirical analysis explores the impact of the intensity of warfare across hundreds of pre-modern polities on sociopolitical complexity,

[5] Related contributions include analyses of the role of intergroup conflict in maintaining cooperation within groups by advantaging more cohesive social formations (Bowles and Gintis 2011), experimental evidence on the role of norm enforcement and punishment in sustaining cooperative behavior (Fehr and Gächter 2002), theories of conflict-driven political consolidation (Carneiro 1970), examinations of warfare and social complexity as drivers of large-scale cooperation (Turchin 2003, 2015), and the political economy of coercive coordination and extraction (Olson 1993).

population scale, and institutional capacity, using panel regressions over long horizons. Yet, despite the breadth of the Seshat Databank, the empirical analysis and the support it lends to the theory are constrained by several substantive limitations.

No Direct Measure of Cooperation

The empirical analysis does not employ a direct measure of cooperation and therefore cannot directly test the theory's central behavioral mechanism. Instead, it evaluates whether periods of heightened intergroup conflict are followed by expansions in state centralization, surplus mobilization, and territorial scale, institutional outcomes that may be correlated with cooperation but serve only as indirect proxies for cooperative behavior.

Survivorship Bias in Historical Samples

The historical sample is unavoidably shaped by systematic selection. The historical record disproportionately reflects societies that prevailed over time, representing cases in which conflict strengthened cooperation and survival. Societies for which conflict yielded collapse or extinction are correspondingly underrepresented, thereby biasing the empirical sample toward cases consistent with the hypothesis.

Correlation Versus Causation

Involvement in intergroup conflict is unlikely to be independent of underlying cooperative capacity.[6] Societies capable of effective coordination were better positioned to prevail in conflict and, for this reason, were also more likely to engage in conflict in the first place. Conflicts, including those triggered by drought, invasions, or other external shocks, therefore cannot be treated as exogenous with respect to pre-existing cooperative predispositions. Observed associations between conflict and cooperation may thus reflect reverse causality as well as unobserved factors that jointly foster cooperation and the incidence of conflict, rather than a causal effect of conflict on cooperative behavior. Moreover, estimating the impact of lagged conflict on proxy indicators of cooperation does not circumvent these identification challenges, since cooperative predispositions persist over time and current predispositions are correlated with their

[6] No-cohesiveness of diverse populations is associated with greater frequency of conflicts (Arbatli, Ashraf, Galor and Klemp, 2020).

past levels. Assessing the causal effect of conflict on cooperation requires disentangling the persistence of underlying cooperative tendencies from any incremental effects attributable to the onset of conflict itself. In the absence of a natural historical quasi-experiment that exposed societies to conflict independently of their predisposition to cooperate, the causal effect of conflict on cooperation cannot be credibly identified.

2.4 The Limits of Conflict-Driven Selection

More fundamentally, however, conflict cannot by itself account for why some societies coordinated with ease while others fragmented under pressure. External danger may have catalyzed collective effort, but it operated on cooperative dispositions that long predated the onset of warfare. These dispositions were not the product of conflict itself. Rather, they emerged unevenly over millennia as human populations adapted culturally to distinct ecological conditions that differentially reinforced orientations conducive to cooperation. In societies where such foundations had taken root, conflict amplified cooperation and channeled it into durable political organization. In contrast, in societies where these predispositions had not developed, conflict was less likely to generate the behavioral substrate required for large-scale coordination, constraining the emergence of complex social structures.

The conflict-based mechanism therefore accounts for how cooperation is scaled in response to external threats, while recognizing that such scaling presupposes deeper cooperative predispositions that long predate the onset of warfare. What, then, are the evolutionary origins of these predispositions and why do they condition whether conflict unifies societies or instead propels them toward social fragmentation?

3. Evolutionary Origins of Cooperative Capacity

Long before warfare magnified the value of cohesion, the foundations of cooperation were shaped by ecological precariousness, where failure to secure resources threatened group viability. In hunter-gatherer societies, ecological volatility heightened the value of cooperation, and behavioral traits that enabled groups to coordinate foraging, share risk, and buffer periods of scarcity, proliferated through cultural transmission. As ecological precariousness was pervasive across early

human environments, selection for cooperative behavior exhibited limited variation across hunter-gatherer groups, sustained by repeated interaction, informal enforcement, reciprocity, and kin-based trust.

Yet, in the course of the Neolithic Revolution, as settlement patterns and subsistence regimes diverged worldwide, environmental pressures became increasingly heterogeneous, thereby generating differential selective pressures across societies. In some regions, environmental pressures shaped a broader set of traits complementary to cooperation, reinforcing existing behavioral dispositions supportive of collective action. In others, the emerging traits were largely orthogonal to cooperation, giving rise to persistent cross-regional variation in the behavioral foundations of large-scale coordination.

In particular, cultural traits such as a future-oriented mindset, restraint, loss aversion, and a predisposition toward parental investment came to play a central role in the scalability and durability of cooperation by anchoring its core requirements. A future-oriented mindset supported investment in public infrastructure; loss aversion fostered mutual insurance; restraint promoted reliability and adherence to norms; and parental investment promoted the skills, trustworthiness, and intergenerational continuity on which stable coordination rests. Environments that fostered these cooperative dispositions generated latent foundations for cooperation beyond kinship, whereas environments less aligned with the emergence of these traits constrained collective action to narrower social circles.

3.1 Foundations of Cooperative Capacity

A broad theoretical tradition has sought to explain the roots of cooperation through cultural evolutionary processes. These frameworks illuminate the mechanisms through which cooperative predispositions emerge, spread, and stabilize within human populations. They underline that cooperative behavior may propagate through social learning and imitation of successful individuals, while being sustained by sanctions and reward structures (Boyd and Richerson 1985, 2005; Richerson and Boyd, 2005; Henrich 2016; Henrich, Richerson, and Boyd, 2016).

Yet these contributions have not examined a central dimension in the evolution of cooperative capacity: the role of cultural adaptation to heterogeneous environments in shaping cross-societal variation in cultural traits conducive to cooperation.[7]

Why did conflict trigger a pronounced expansion of cooperation in some societies, yet yield far weaker or even destabilizing outcomes in others? What role does variation in human cultural adaptation across ecological niches play in shaping the cooperative predispositions that mediate the impact of conflict on coordination? This foundational layer is central to understanding the conditions under which conflict amplified cooperation, as well as the circumstances in which it instead exposed latent vulnerabilities.

3.2 Adaptive Origins of Cooperative Traits

What agroecological conditions led some societies to develop and reinforce cultural traits conducive to cooperation? Tracing the roots of cooperation hinges on identifying ancestral environments conducive to the emergence of these cultural predispositions.

Foundational cultural traits underlying cooperation differ markedly across societies, reflecting variation in the agroecological environments in which these behavioral traits were formed, prior to the emergence of complex states, formal institutions, or sustained intergroup warfare. Human adaptation to diverse ecological niches profoundly shaped the emergence of behavioral traits that, in some environments, complemented and enabled cooperative predispositions beyond kinship. Culturally transmitted social dispositions aligned with prevailing ecological conditions enhanced household resilience in Malthusian environments, allowing these orientations to persist and diffuse across generations.[8] When environment-specific pressures reinforced predispositions supporting investment in future productive capacity, stabilizing consumption across seasons, reducing exposure to catastrophic losses, or strengthening the intergenerational transmission of skills, these traits became more prevalent within local populations. Conversely, when such dispositions were poorly suited to local constraints, alternative behavioral tendencies better aligned with those

[7] Differential adaptability may arise from heterogeneity in the environment or from diversity within the human population (Ashraf and Galor, 2013).

[8] Societies with greater inherited cultural diversity adapt more effectively to local ecological conditions, as a broader range of initial cultural predispositions increases the likelihood that behaviors complementary to prevailing environments are selectively reinforced over time. When ecological conditions reward coordinated action, this adaptive process makes the emergence and persistence of cooperative orientations more likely in more diverse populations (Galor, Klemp and Wainstock, 2026).

constraints gained traction. Over time, this process of cultural adaptation generated enduring regional differences in behavioral traits, shaping the capacity to scale cooperation once institutional development and intergroup conflict intensified.

Four traits that emerged in response to distinct environmental pressures are particularly consequential for the emergence of cooperation: a future-oriented mindset, restraint, loss aversion, and predisposition toward parental investment in offspring. A future-oriented mindset supported investment in shared infrastructure; loss aversion facilitated mechanisms of mutual insurance; restraint promoted reliability and adherence to cooperative norms; and parental investment in offspring cultivated the skills, trustworthiness, and intergenerational continuity on which stable coordination rest.[9]

Future-Oriented Mindset and Restraint

The adaptive reinforcement of a future-oriented mindset and a greater predisposition toward restraint depended on the relative returns to agricultural investment across agroecological settings. While humans had already evolved a distinctive cooperative psychology long before the advent of agriculture, regions where agroclimatic conditions supported crops with high potential caloric yields offered stronger incentives for deferring consumption in favor of planting, cultivating, and storing. In such environments, behavioral propensities grounded in future orientation and restraint supported household prosperity and were therefore more likely to persist and diffuse across generations through vertical and horizontal cultural transmission (Galor and Özak 2016).[10]

Loss Aversion

Climatic volatility shaped culturally transmitted orientations toward losses by elevating catastrophic losses, rather than forgone gains, as the primary threat to survival. In environments characterized by greater climatic volatility, households that adopted production strategies less vulnerable to adverse fluctuations were more likely to maintain subsistence and secure continuity across generations, whereas those guided by more loss-neutral orientations faced a higher risk of

[9] Talhelm et al. (2014) and Galor and Özak (2016).

[10] Culture–language coevolution gave rise to the evolution of complementary linguistic features, such as the grammatical encoding of the future tense (Galor, Özak and Sarid, 2025).

disruption or disappearance when conditions turned unfavorable. Over time, societies exposed to climatic shocks that were widespread across entire regions**,** and therefore difficult to insure through local diversification, tended to develop a stronger predisposition toward loss aversion. In contrast, societies facing predominantly localized or idiosyncratic climatic shocks**,** which could be buffered through spatial diversification or exchange, tended to favor more loss-neutral orientations. These predispositions persisted and diffused through vertical and horizontal cultural transmission, reinforcing enduring regional differences in loss-related behavioral traits (Galor and Savitskiy 2022).[11]

Predisposition toward investment in offspring

Biogeographical conditions that facilitated an earlier onset of the Neolithic Revolution and thus an earlier transition to sedentary agricultural communities laid the foundations for markets and trade, thereby raising the long-run return to human capital. In these environments, literacy, numeracy, mechanical aptitude, agronomic knowledge, and tool use increased productivity, and cultural orientations favoring parental investment yielded greater intergenerational prosperity. As families that invested more intensively in their children achieved greater economic success and long-run viability, and as vertical and horizontal transmission reinforced these orientations, a predisposition toward parental investment became increasingly prevalent within these populations (Galor and Moav, 2002, and Galor and Klemp, 2019).

3.3 Agroecological Roots of Large-Scale Cooperative Capacity

Ecological conditions operating through time preference, restraint, loss orientation, and the returns to skill generated enduring differences in the social dispositions that underlie cooperation. In some environments, a future-oriented mindset, restraint, loss aversion, and parental investment supported more stable economic conditions and were transmitted through cultural channels, creating behavioral inclinations capable of sustaining cooperation beyond kinship. In others, where

[11] This pattern is supported by evidence linking historical climatic volatility to contemporary variation in loss aversion across countries, regions, and ethnic groups, including among second-generation migrants whose attitudes reflect the climatic conditions of their ancestral homelands. A related culturally adaptive development was the rise of an entrepreneurial orientation in settings that reinforced experimentation and rewarded innovative activity (Galor and Michalopoulos, 2012).

short-term payoffs dominated and trust remained localized, predispositions conducive to large-scale coordination were less likely to emerge or persist.

This ecological foundation shaped both a society's propensity to engage in conflict and the manner in which it responded to it. In environments where ecological adaptation had produced long-term orientation, trust, reciprocal norms, and disciplined coordination, conflict could have amplified cooperation, enabling the emergence of taxation, irrigation systems, bureaucratic capacity, and proto-state structures. In settings where ecological conditions had yielded short horizons, fragmented trust, and limited capacity for coordinated action, conflict was more likely to magnify fracture and contribute to societal collapse. War magnified cooperative capacity where its cultural building blocks existed, while deepening division where such foundations had not been formed.

Just as importantly, the ecological orientations that underpinned cooperation also shaped which societies engaged in conflict. Groups characterized by future orientation, reciprocal discipline, and large-scale coordination were more likely to participate in territorial competition and warfare because these culturally reinforced orientations lowered the costs of mobilization and made coordinated action more attainable. In contrast, societies lacking these foundational orientations often remained insulated from such engagements, as the high cost of mobilization made large-scale collective action unlikely. Thus, the observed association between conflict and cooperation may, at least in part, reflect the influence of culturally shaped cooperative orientations on the likelihood of conflict itself.

As long as societies differ markedly in their cooperative substrates, the effect of conflict on cooperative capacity is not only empirically difficult to identify but conceptually ambiguous. Conflict does not operate on homogeneous populations; it acts on culturally heterogeneous foundations that shape both its emergence and its consequences. Without a mapping of the global distribution of these predispositions, observed associations cannot distinguish whether conflict amplified cooperation or merely arose in societies where cooperative orientations were already in place.

Identifying the origins of variation in this foundational layer is essential not only for uncovering cross-societal differences in cooperative capacity, but also for determining whether subsequent forces such as warfare or intergroup competition genuinely amplified cooperation or merely operated through selection among societies with pre-existing cooperative predispositions. Absent

such grounding, empirical attempts to estimate the impact of warfare on cooperation risk conflating pre-existing cooperative foundations with the mechanisms that later expanded them. Conflict is more likely to amplify cooperation where such foundations exist, while in their absence conflict may erode social trust, intensify fragmentation, or reinforce narrow, kin-based forms of cooperation, thereby limiting effective mobilization and institutional development.

Groups whose dispositions for coordination were limited lacked not only the basis for large-scale cooperation but also the conditions that would have enabled them to initiate or sustain conflict. Their persistent non-cooperative orientations reflected the absence of cultural foundations required for both mobilization and conflict-driven selection, underscoring that conflict is endogenous to cooperative capacity. Conflict magnified coordination where such foundations existed and rarely arose where they remained underdeveloped.

4. A Unified Framework for Understanding Conflict and Cooperation

Large-scale cooperation emerged from the interaction between two distinct evolutionary layers: a foundational layer shaped by long-run ecological and cultural adaptation, and an expansionary layer driven by intergroup conflict and institutional consolidation. In Turchin (2025)'s account, conflict acts as a selective and amplifying force that reinforces cooperation. Intergroup competition intensifies coordinated action, fosters discipline, and selects for institutional arrangements capable of sustaining large-scale coordination, thereby contributing to the institutional scaffolding of the state. In this formulation, warfare constitutes a primary force in the scaling and stabilization of cooperation and a major source of institutional development.

Yet conflict operated on uneven pre-existing behavioral predispositions toward cooperation. Cooperative predispositions forged in the course of cultural adaptation to differential ecological conditions varied markedly across societies and governed both the likelihood of conflict and its observed consequences. If such predispositions were uniform across societies, the relationship between conflict and cooperation would be largely invariant across settings. When cooperative capacity varies across populations, however, conflict is more likely to arise, persist, and succeed in societies where coordination was already feasible. Observed associations between conflict and

cooperation therefore conflate the effects of conflict with persistent underlying heterogeneity in cooperative capacity.

In the spirit of Unified Growth Theory (Galor 2011),[12] the evolution of cooperation ought to be explored within a unified framework that integrates both layers of its historical formation. Abstracting from this two-stage process in the evolution of the predisposition toward cooperation, and in particular from the uneven distribution of cooperative capacity that emerged in the foundational layer**,** yields an incomplete and potentially inaccurate account of conflict-driven cooperation. The onset of conflict is endogenous to cooperative predispositions, acting as a catalyst that reinforces and scales cooperation where such foundations have taken root, while magnifying fragility and division where they remain shallow or absent.

5. Rethinking the Arc of Cultural Evolution

The ascent of large-scale cooperation laid the foundations for technological progress, scientific inquiry, and the rise of cities, states, and empires. Yet cooperative capacity did not emerge uniformly across societies. Its origins preceded recorded history and were shaped gradually by ecological and subsistence conditions that favored distinct and enduring cooperative dispositions. In some regions, these conditions encouraged patience, reciprocity, and disciplined coordination, enabling cooperation beyond kinship; in others, ecological pressures kept coordination largely confined within the clan.

Conflict, along with hierarchical organization and growing demands for public infrastructure, played a significant role in shaping cooperation over the course of human existence, yet its effects were decisively conditioned by behavioral foundations rooted in long-run cultural adaptation. Conflict intensified cooperative capacity where such foundations existed and exposed latent vulnerabilities where they were fragile. In populations where cooperative dispositions had taken root, conflict, and the associated demands of hierarchy, extraction, and shared infrastructure, catalyzed their expansion into structured forms of collective organization. Conversely, in societies with weaker orientations toward cooperation, conflict was seldom advantageous, and when it occurred, it often intensified existing divisions, at times precipitating destructive outcomes and

[12] See also Galor (2005, 2010, 2022, 2025).

societal collapse. Seen through this lens, conflict functioned less as a generator of cooperation than as a force that revealed and amplified preexisting cultural variation.

Intergroup conflict and institutional development provided the arena in which preexisting cultural orientations toward collective action were consolidated and formalized. In populations where ecological adaptation had already cultivated patience, reciprocity, and the capacity for disciplined coordination, conflict and institutional development channeled these orientations into codified norms, stable administrative structures, and broader systems of mutual obligation. In contrast, in settings in which such social propensities had not been formed, rallying groups for sustained collective action was far more challenging, and episodes of conflict frequently aggravated existing internal rifts rather than producing cohesion or durable organizational forms.

Exploring the empirical relationship between conflict and cooperation poses therefore formidable challenges. The onset of conflict is itself shaped by pre-existing cooperative predispositions, and observed associations between conflict and cooperation may therefore reflect reverse causality and unobserved forces that jointly govern cooperative capacity and the incidence of conflict. In the absence of a mapping of pre-existing cross-societal variation in cooperative predispositions, the effect of conflict on cooperation would remain elusive, as it would be infeasible to resolve the fundamental question of whether conflict amplified cooperation or merely unfolded disproportionately in societies in which cooperative predispositions had already crystallized.

6. Concluding Remarks

The rise of large-scale cooperation was deeply uneven and contingent on pre-existing cultural foundations. It unfolded as a two-phase process. In the adaptation phase, cultural evolution generated uneven capacities for coordination across societies, whereas in the expansionary phase, the evolution of cooperation acted upon this uneven terrain, strengthening cooperation where cooperative foundations had taken root, while revealing fragility where they were weak or absent. Rather than treating intergroup conflict, political stratification, and the growing demand for shared infrastructure as independent drivers of cooperation, the proposed analytical framework views them as endogenous expansionary forces that operated on pre-existing, yet unevenly distributed cooperative predispositions. These forces revealed, magnified, and selected among inherited cultural orientations toward cooperation, while amplifying fragility and division where cooperative foundations had yet to crystallize. The proposed framework therefore accounts for the

coexistence of enduring institutional formation alongside episodes of recurrent societal collapse across human history.

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