

War, space, and the evolution of Old World complex societies

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How did human societies evolve from small groups, integrated by face-to-face cooperation, to huge anonymous societies of today, typically organized as states? Why is there so much variation in the ability of different human populations to construct viable states? Existing theories are usually formulated as verbal models and, as a result, do not yield sharply defined, quantitative predictions that could be unambiguously tested with data. Here we develop a cultural evolutionary model that predicts where and when the largest-scale complex societies arose in human history. The central premise of the model, which we test, is that costly institutions that enabled large human groups to function without splitting up evolved as a result of intense competition between societies—primarily warfare. Warfare intensity, in turn, depended on the spread of historically attested military technologies (e.g., chariots and cavalry) and on geographic factors (e.g., rugged landscape). The model was simulated within a realistic landscape of the Afroeurasian landmass and its predictions were tested against a large dataset documenting the spatiotemporal distribution of historical large-scale societies in Afroeurasia between 1,500 BCE and 1,500 CE. The model-predicted pattern of spread of large-scale societies was very similar to the observed one. Overall, the model explained 65% of variance in the data. An alternative model, omitting the effect of diffusing military technologies, explained only 16% of variance. Our results support theories that emphasize the role of institutions in state-building and suggest a possible explanation why a long history of statehood is positively correlated with political stability, institutional quality, and income per capita.

cultural evolution | social complexity | ultrasociality

Humans have the ability to live and cooperate in huge groups of genetically unrelated individuals (what can be termed “ultrasociality”) (1, 2). The central conceptual issue that this paper addresses is what mechanisms facilitate the spread of the necessary norms and institutions that enable human groups to function at the scale of millions of individuals (3–5). Social scientists have proposed a number of theories to explain the emergence of large-scale societies, emphasizing such factors as population growth, warfare, information management, economic specialization, and long-distance trade (6–10). However, because existing theories are usually formulated as verbal models, the causal mechanisms underlying these theories are not always made explicit. Understanding how ultrasocial norms and institutions spread is not a simple matter of their benefits for large-scale societies. Collective action problems, which stem from the tension between public nature of benefits yielded by cooperation and private costs borne by cooperating agents (11), inevitably arise when large groups of people need to cooperate in the production of public goods. Any theory that does not explain how societies find ways to solve these problems must be incomplete.

Ultrasocial Norms and Institutions

Social norms and institutions are among the most important ways of solving the collective action problem (4, 12, 13). Although much theory building has focused on solving cooperative dilemmas within groups of individuals, collective action problems

can arise at all levels of organization (14). For example, an archaic state may arise when several chiefdoms are unified (by conquest, by dynastic marriage, etc.). In order for the state to function well and preserve its integrity, its constituent units (formerly chiefdoms, now provinces) have to cooperate with each other (at the very least, the regional elites need to cooperate with the center).

As an example of an ultrasocial norm, consider generalized trust (14). Propensity to trust and help individuals outside of one's ethnic group has a clear benefit for multiethnic societies, but ethnic groups among whom this ultrasocial norm is widespread are vulnerable to free-riding by ethnic groups that restrict cooperation to coethnics (e.g., ethnic mafias). An example of an ultrasocial institution, much discussed by historians and political scientists, is government by professional bureaucracies (15). Other examples include systems of formal education, with the Mandarin educational system in China as the most famous example, and universalizing religions. World religions first appeared during the Axial Age (16) and provided a basis for integrating multiethnic populations within first mega-empires, such as Achaemenid Persia (Zoroastrianism), Han China (Confucianism), and Maurya Empire (Buddhism).

Our theoretical framework for understanding the evolution of social norms and institutions is provided by cultural multilevel selection (CMLS) (5, 17). Because the benefits of ultrasocial institutions are only felt at larger scales of social organization, and costs are born by lower-level units, fragmentation into lower-level units often leads to a loss of such institutions. For example, when a territorial state fragments into a multitude of province-sized political units, ultrasocial institutions such as governance by professional bureaucracies or education systems producing literate elites may be gradually lost (as happened, e.g., in parts of

Significance

How did human societies evolve from small groups, integrated by face-to-face cooperation, to huge anonymous societies of today? Why is there so much variation in the ability of different human populations to construct viable states? We developed a model that uses cultural evolution mechanisms to predict where and when the largest-scale complex societies should have arisen in human history. The model was simulated within a realistic landscape of the Afroeurasian landmass, and its predictions were tested against real data. Overall, the model did an excellent job predicting empirical patterns. Our results suggest a possible explanation as to why a long history of statehood is positively correlated with political stability, institutional quality, and income per capita.

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western Europe after the collapse of the Roman Empire). Costly ultrasocial institutions can evolve and be maintained as a result of competition between societies: societies with traits that enable greater control and coordination of larger numbers will out-compete those that lack such traits (2, 18–20). Although societies can compete in many ways, here we focus entirely on warfare. Thus, our theoretical prediction is that selection for ultrasocial institutions and social complexity is greater where warfare between societies is more intense.

Historically one of the most important factors determining the intensity of Afroeurasian warfare was proximity to grasslands inhabited by horse-riding nomads (21–24). Steppe nomads influenced the dynamics of agrarian societies both directly, by eliminating weaker and less cohesive states (25), and indirectly, by innovating and spreading technologies that intensified warfare—most notably, chariots, horse-riding, and stirrup/heavy cavalry (26). These innovations were eagerly adopted by agrarian states so that new, intense forms of offensive warfare diffused out from the steppe belt. Our hypothesis, therefore, focuses on the interaction between ecology/geography and the historically attested development of military innovations. To test this idea, in this paper we develop a cultural evolutionary model that predicts where and when the largest-scale complex societies arose in human history.

The Model

We developed a spatially explicit, agent-based simulation that translates these theoretical principles into quantitative predictions. Our approach is therefore somewhat different from the traditional method of inquiry that historians use. Mathematical models are an important part of any mature science and serve a number of useful purposes. First, by testing the logic of the proposed mechanisms and making the assumptions explicit, such models allow us to evaluate whether our theory provides a possible explanation of the emergence of large-scale complex societies. Second, the model can yield sharply defined, quantitative predictions that can be unambiguously tested against data. By comparing data from our simulations with real data on the historical distributions of large states and empires, we can test whether the model offers a plausible explanation. Most importantly, we can also investigate whether alternative hypotheses are equally as good at explaining the observed data.

We build on our earlier theoretical work (27), making it more realistic by explicit consideration of culturally transmitted traits and geography; this enables us to assess how well our model explains observed historical distributions of large-scale societies. The modeled landscape is the Afroeurasian landmass divided into a grid of 100×100 -km squares (*SI Appendix*). Each grid cell is characterized by existence of agriculture, biome (e.g., desert), and elevation. At the beginning of the simulation, each agricultural square is inhabited by an independent polity, and the cells adjacent to the steppe are “seeded” with military technology (MilTech) traits, which gradually diffuse out to the rest of the landmass.

As explained above, the core of the model is the dynamics of ultrasocial traits (norms and institutions) (13). Each cell is inhabited by a community that has a “cultural genome,” a vector taking values of 1 or 0, depending on whether an ultrasocial trait is present. An ultrasocial trait can be gained in a community. However, because such traits are costly, the probability of losing an ultrasocial trait is much greater. Thus, in the absence of other evolutionary forces, ultrasocial traits would be present in the landscape at a very low frequency.

The force that favors the spread of ultrasocial traits is warfare. Agricultural cells can conquer other such squares, building multicell polities. The probability of winning depends on relative powers of the attacking and defending polities, with power determined by the polity size (number of cells) and the average number of ultrasocial traits. When a cell from the defeated polity is annexed, the losing cell may copy the cultural genome of the victor. This change reflects either the victorious society imposing

its culture on the defeated (e.g., by religious conversion, linguistic assimilation, or replacing literate elites of the defeated group) or the physical removal of individuals (e.g., genocide, expulsion); however, this is not essential in the case of culturally transmitted traits. The probability of such replacement increases with the number of MilTech traits; more effective forms of offensive warfare make victory more decisive. The conceptual core of the model invokes the following causal chain: spread of military technologies→intensification of warfare→evolution of ultrasocial traits→rise of large-scale societies.

Our simulations are run on a map that includes other important aspects of real-world ecology. Mountainous terrain (proxied by elevation) is easier to defend and less likely to be effectively controlled (28, 29), which increases the probability of more mountainous locations successfully repelling attacks and decreases the probability that defeated cells will copy the traits of their conquerors (*SI Appendix*).

Empirical Tests of the Model Predictions

We tested how good the model was at predicting the historical distributions of large-scale societies in Afroeurasia during 1,500 BCE–1,500 CE. Using a geographic information system and the same grid as in the simulation (we sampled model output in precisely the same way as data), we compiled information from a variety of historical atlases and other sources to draw maps at 100-y intervals of all polities that controlled territories greater than $\sim 100,000$ km² (*SI Appendix*). Next, we created imperial density maps indicating the frequency and distribution of large-scale societies; i.e., we calculated how often each grid cell was found within a large-scale polity. To capture changes through time, we examined imperial density maps for each of the three millennia. Thus, the model was tested for its ability to predict a large dataset—7,941 empirical points (each of the 2,647 agricultural cells for three eras).

As Fig. 1, *SI Appendix*, and *Movie S1* show, our model is able to produce outputs that are remarkably similar to the observed data. As in the real data, the first imperiogenesis hotspots appear in Mesopotamia, Egypt, and North China because these areas are situated near the steppe frontier, and that is where MilTech diffuse first, tipping the selection in favor of ultrasocial traits. A sufficient frequency of ultrasocial traits, then, enables the rise of large and relatively stable states. Fig. 2 shows that the density of ultrasocial traits is closely correlated with imperial density. Macrostate formation then occurs when MilTech traits diffuse to the central Mediterranean/western Europe, north India, and South China, and yet later to northern and eastern Europe, Japan, Southeast Asia, and Sub-Saharan Africa. Model dynamics, thus, reflect the historical pattern of such innovations as chariots and cavalry first spreading to regions proximate to the steppe, and later to more distant regions. It should be noted that though Egypt is not directly adjacent to the Eurasian steppe belt (which extends into central Anatolia), it is close enough that MilTech traits diffuse there by the middle of the first era (1,500–500 BCE); historically, this corresponds to the spread of chariot warfare to Egypt by the Hyksos, and later the spread of cavalry, which first appears with the raiding Scythians (30). Furthermore, there is also a close correlation between the appearance of such innovations and subsequent rise of large-scale states (25) (Fig. 3A).

We assessed quantitatively how well our model fits the historical data, and investigated whether simpler processes could generate these patterns. A quantitative measure of fit suggests that under certain parameter values the model can explain two-thirds of the variance in overall imperial density (Table 1 and *SI Appendix*). R^2 values are also substantial for each era. This is a striking result, given that the model with 12 parameters (of which only four have substantial effects on model performance) is predicting 7,941 data points. Model predictions do not depend sensitively on precise parameter values ($R^2 \sim 0.5$ or better for a broad range of parameters; *SI Appendix*). However, turning off the effect of elevation reduces model accuracy, whereas making

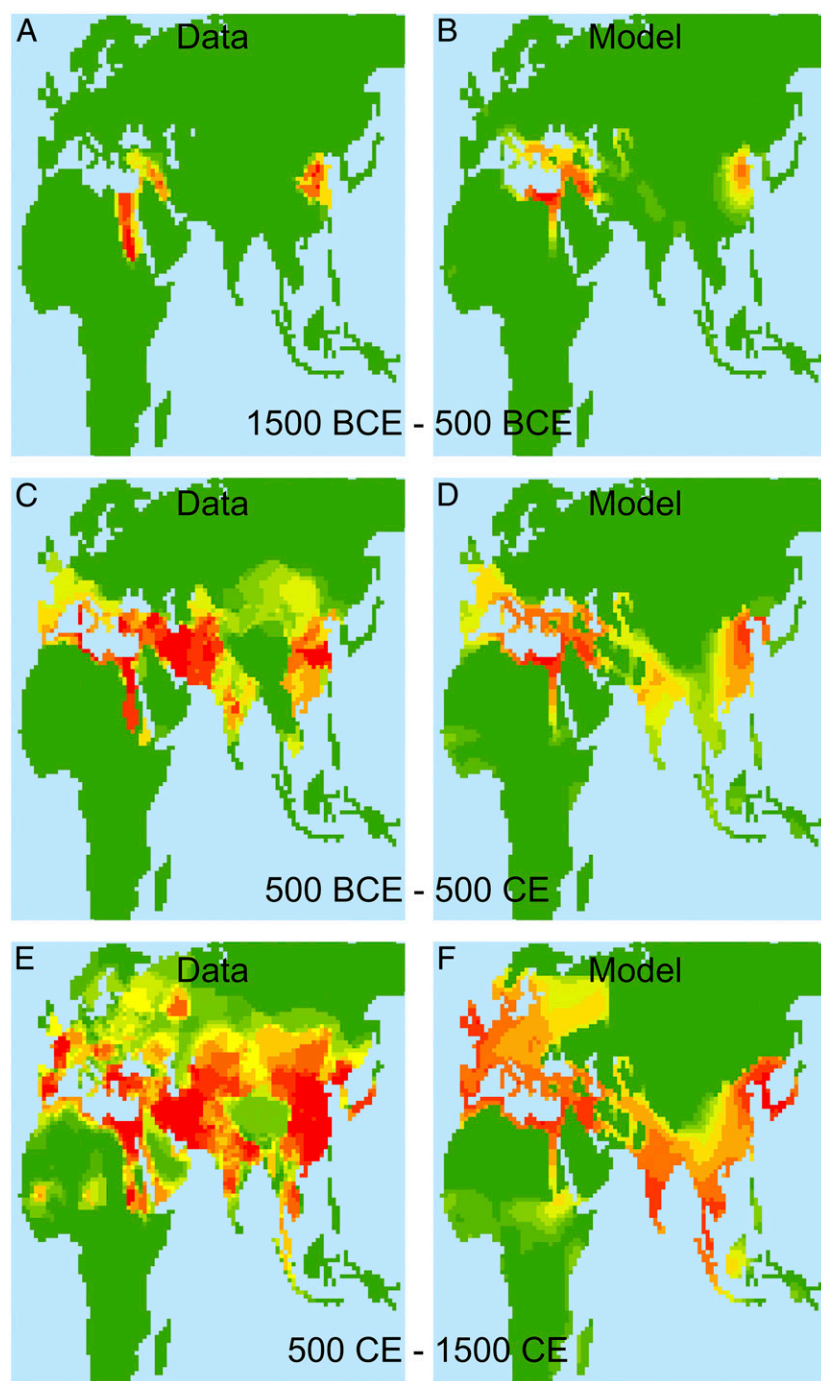


Fig. 1. Comparison between data (A, C, and E) and prediction (B, D, and F) for three historical eras. Model predictions are averages over 20 realizations. Red indicates regions that were more frequently inhabited by large-scale polities, yellow shows where large polities were less common, and green indicates the absence of large polities during the period.

warfare equally intense everywhere (no effect of MilTech) or seeding MilTech randomly (instead of on the steppe interface) results in an almost complete loss of predictability (Table 1). This result shows that the match between the model and the historical data is not simply an artifact of the particular shape of the grid in which we run our model. It appears that the diffusion of MilTech and its effect on warfare intensity did indeed create an important selective force favoring the emergence of larger-scale societies. Not including these processes in the model produces results that do not match the historical data.

The importance of the steppe frontier in the evolution of ultrasociality is supported by spatially explicit statistical analyses of imperial density maps. Simultaneous autoregressive models (SAR), which account for spatial autocorrelations in the data

(31), show that the distance from the steppe is the strongest predictor of total imperial density in agricultural cells (Fig. 3B), followed by a measure of the long-term presence of agriculture in these cells, and elevation (*SI Appendix*). These three variables predict 42% of the variance in these models. Interestingly, the estimated historical distribution of horse-based warfare involving chariots and cavalry is also a good predictor of imperial density, which is consistent with our assumption that more intense forms of warfare act as an evolutionary driver of social complexity.

Discussion

Historians have traditionally focused on reconstructing the specific historical development of individual polities or regions. Our approach here is very different. We have made use of historical

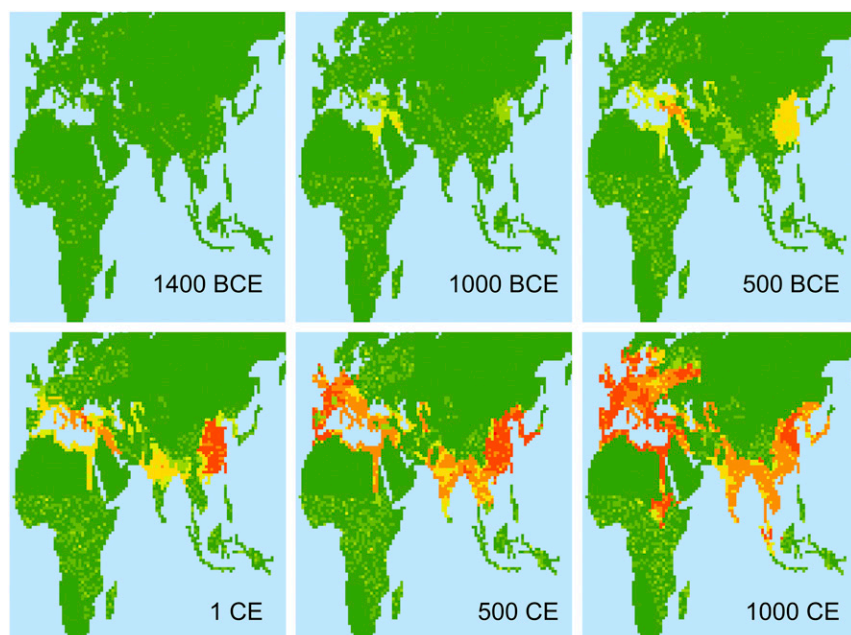


Fig. 2. Dynamics of ultrasocial trait density in one realization of the model. Note the initially random distribution of ultrasociality traits. As in Fig. 1, red indicates high density of ultrasocial traits and green their absence.

information to build up a more general, composite picture of the historical and geographical locations of large-scale societies. The model developed here does well at predicting the broad outlines of where and when such societies have traditionally formed and persisted. This is a remarkable result, given the limitations of historical data and a rudimentary representation of the environment and the causal mechanisms in the model. Due to the nature of the question addressed in our study, there are inevitably several sources of error in historical and geographical data we have used. However, it is important to note that these errors are not biased toward providing support for our particular hypothesis. Our use of a regular sampling strategy is a strength that allows us to collect data in a systematic way independent of the hypothesis being tested rather than cherry-picking examples that support our ideas. We have also chosen to focus on agrarian societies during a particular timeframe and in a particular part of the world. Future work will extend this approach to examine the evolution of social complexity in the Americas and in the Old World after 1,500 CE (*SI Appendix, Supporting Discussion*).

Despite the current dominance of societies with origins in western Europe, our data indicate that for most of recorded history, Egypt, the Near East, Central Asia, and China were the predominant imperial hotspots. We have argued here that this pattern was due to the emergence and spread of technologies enabling more intense forms of warfare that, in turn, created selection pressures for the cultural evolution of norms and institutions, making possible cooperating groups numbering in the millions. In our model, the key mechanism is the elimination of groups and societies that fail to acquire/retain ultrasocial institutions via a process of CMLS. Because the intensity of between-group competition varies in space and time, we were able to test the model's predictions empirically. Recent research indicates that there are strong empirical patterns linking history and geography to the current distribution of world wealth and political stability (*SI Appendix, Supporting Discussion*). Our model provides a possible explanation of how history and geography can interact in enabling the spread and persistence of ultrasocial institutions. For example, the presence of agriculture is partly due to the suitability of external environmental conditions, and partly due to the development and spread of agricultural techniques and technologies through population expansion and cultural transmission. Military technology spreads via cultural transmission, yet the most important aspect of this factor was that the location of its initial development was on the ecological boundary of the

Eurasian steppe (which itself was due to a historical contingency—availability of wild horses for domestication). In turn, this may explain why factors relating to countries' economic and political development, including institutional quality and even income per capita, show positive associations with a long history of statehood (32).

More generally, the present study highlights the role that evolutionary theory in combination with suitable data can play in addressing questions about human history and cultural evolution. Undoubtedly, the rise and fall of individual states and empires will be complex, involving idiosyncratic and contingent events. Our analyses, however, also provide support for the idea that the story of the past is not just a case of "one damned thing after another" (33), but that there are general mechanisms at play in shaping the broad patterns of history (34–36).

Methods

General Logic of the Model. The goal of the model is to understand under what conditions ultrasocial norms and institutions will spread. The theoretical framework is provided by CMLS (5, 17). As explained previously, within-group forces cause ultrasocial traits to collapse and to be replaced with noncooperative traits. However, ultrasocial traits increase the competitive ability of groups. Thus, if selection between groups is strong enough, ultrasocial traits should spread despite being disadvantaged within groups.

The strength of between-group competition is assumed to be affected by two broad groups of factors: technology and geography. The two technological factors that we consider explicitly are productive (agricultural) technologies and military technologies. For simplicity, agriculture is modeled as a binary variable (presence or absence of intensive agriculture capable of supporting a complex society). Presence of agriculture is a necessary condition for a cell to attack or be attacked and potentially annexed.

Military technologies (note the plural) directly affect the strength of between-group competition; each is also modeled as a binary variable. The more such technologies are present in an area, the greater the probability that a successful attack will be decisive enough to result in cultural extinction of the losing group, and cultural domination by the victorious group.

The model assumes that military technologies arise on the interface between the Eurasian steppe belt and agrarian societies living next to it. This assumption is meant to capture the pattern of invention and spread of military innovations during the era when horse-related military innovations dominated warfare within Afroeurasia (after the introduction of the chariots and before the widespread use of gunpowder; thus, roughly 1,500 BCE to 1,500 CE). As military historians have documented (26, 37), these innovations included chariots, mounted archery, heavy cavalry, and stirrups, among others. We are not arguing that horse-related innovations were the only

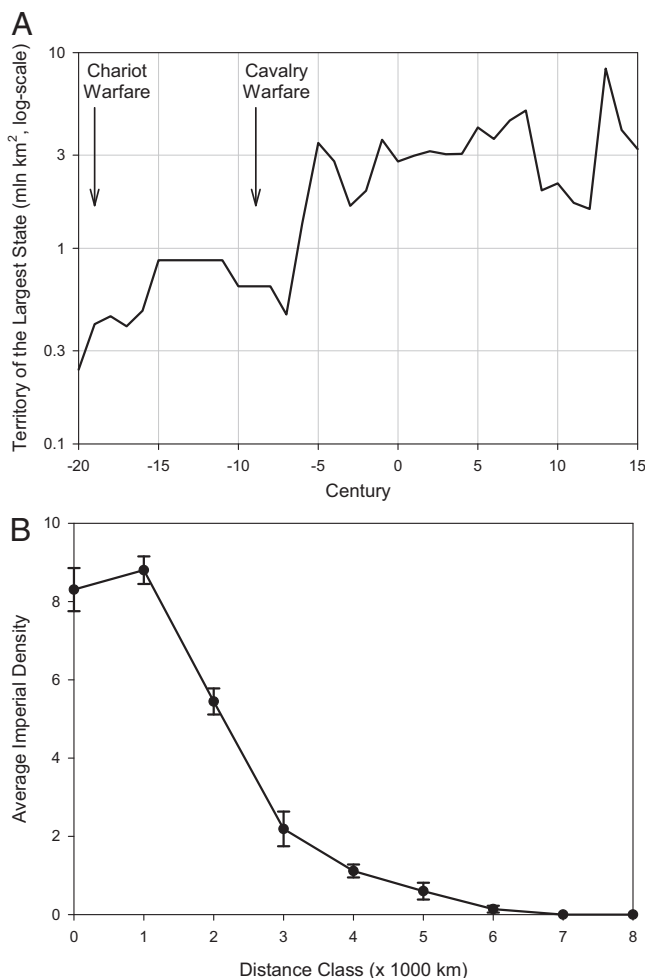


Fig. 3. Strong temporal and spatial patterns in the data. (A) Invention of chariots and cavalry revolutionized warfare and led to lasting increases in the scale of social integration (pre-1,500 BCE data from ref. 25). (B) Imperial density decreases with increasing distance from the steppe (distance classes: 0 = within the steppe; 1 = 1–1,000 km, and so on; error bars indicate 95% confidence interval).

ones important in premodern warfare; rather, the argument is that the arrival of such technologies in an area significantly elevates the intensity of between-polity competition above existing levels. Thus, the model focuses not on the evolution of any kind of state, but on the rise and spread of very large states: macrostates. Our hypothesis is that the diffusion of horse-related military technologies from the steppe-sown interface to the rest of Afroeurasia results in a characteristic spatiotemporal pattern of spread of intense forms of warfare, leading to macrostate forms of political organization.

Other military innovations, such as the use of metals for weapons and armor, were often “bundled” with horse-based technologies. For example,

Table 1. Effect of turning off various components of the model on its ability to predict data (R^2 for each era, and overall R^2)

Model	Era 1	Era 2	Era 3	Overall
Full model	0.56	0.65	0.47	0.65
No elevation effect ($\gamma = \gamma_1 = 0$)	0.31	0.46	0.35	0.48
No effect of MilTech on ethnocide ($\epsilon_{\min} = \epsilon_{\max}$)	0.08	0.08	0.02	0.16
No effect of the steppe (MilTech seeded randomly)	0.03	0.11	0.00	0.17

the use of iron arrowheads significantly increased the killing power of mounted archers, and better metal-working techniques (and, later, the spread of the stirrup) led to heavy cavalry. All such innovations are modeled simply as abstract “military technologies.”

Unlike technology, the geographic variables we model do not change with time (we assume that the climate change over the modeled period can be safely ignored). The features of geography that are explicitly taken into account are (i) deserts and steppes (modeled as lacking agriculture in the time period considered here), (ii) mountains (elevation), (iii) rivers (make agriculture possible when flowing through deserts), and (iv) sea coasts (coastal cells can also initiate attacks against other coastal cells within a certain distance). The extent of agriculture is modeled as changing during the simulation to reflect the historical spread of agricultural populations and technologies (SI Appendix).

Only agricultural cells are explicitly modeled. Each agricultural cell is occupied by a local “community.” Each community is characterized by two binary vectors of cultural traits. The first one, U , contains n_{ultra} ultrasociality traits and the second one, M , contains n_{mil} of MilTech traits. Thus, $u_{i,x,y}$ is the value of the i th ultrasociality trait for the community located at (x, y) coordinates, and $m_{i,x,y}$ is the same for MilTech traits. Both ultrasociality and MilTech traits take values of either 0 (absent) or 1 (present).

Each community (agricultural cell) has up to four land neighbors (thus, cells touching corners diagonally are not considered to be neighbors). Cells neighboring on sea (“littoral cells”) can also interact with other nearby littoral cells (this will be explained below). Time is discrete.

Communities are aggregated within multicell polities. A polity can also consist of a single community. At the beginning of the simulation, all polities start with just one cell. Polities engage in warfare that, if successful, can result in victors conquering cells from other polities. Polities can also disintegrate. Ultrasociality traits characterizing each community can change by mutation, or by cultural assimilation (ethnocide), whereas MilTech traits change by diffusion. These processes are described in greater detail below.

Warfare. Warfare between polities occurs at the boundaries between them. Border cells (cells with at least one neighbor belonging to a different polity) are randomly sampled to select an attacker, which attempts attack in a randomly chosen direction. If the defending cell belongs to a different polity, warfare between the two polities is initiated with probability P . All border cells receive one chance to initiate attack in a year, but the order in which they are chosen is randomized every time-step. This sampling scheme implies that the probability of attack by one polity on another is proportional to the length of the boundary between them.

Littoral cells can also initiate a seaborne attack. If such a cell attempts to attack a sea cell on which it borders, the simulation checks whether there are any other littoral cells within the distance d_{sear} , and if yes, proceeds to attack such a cell in the usual manner.

The success of attack is determined by the relative powers of the attacking and defending polities. The power of attacker depends on its average level of ultrasociality (the average number of ultrasociality traits in its communities):

$$\bar{U}_{\text{att}} = \frac{\sum_j \sum_i u_{ij}}{S_{\text{att}}},$$

where u_{ij} is the value (0 or 1) of ultrasociality trait in the i th locus of j th community belonging to the polity and S_{att} is the polity size (the number of communities).

Both average ultrasociality level and size increase a polity’s power:

$$P_{\text{att}} = 1 + \beta \bar{U}_{\text{att}} S_{\text{att}}.$$

Here, β is the coefficient that translates ultrasociality traits into the polity’s power. Thus, if no community within the polity has any ultrasocial traits, the polity’s power will be at the minimum, 1. If, however, all communities have all possible ultrasociality traits, then the polity power will be at maximum, or $1 + \beta n_{\text{ultra}} S_{\text{att}}$, where n_{ultra} is the number of traits (length of the ultrasociality vector).

The power of the defending polity similarly increases with its size and average number of ultrasociality traits. Because mountainous areas are easier to defend, the defender’s power is increased by the elevation of the defending cell:

$$P_{\text{def}} = 1 + \beta \bar{U}_{\text{def}} S_{\text{def}} + \gamma E_{\text{def}},$$

where E_{def} is the elevation (in kilometers) of the defending cell found at spatial coordinates x and y , and γ is the coefficient translating elevation into defensive power.

The probability of successful attack is then calculated according to the following formula:

$$P_{\text{success}} = \frac{P_{\text{att}} - P_{\text{def}}}{P_{\text{att}} + P_{\text{def}}}$$

If $P_{\text{success}} < 0$ (that is, $P_{\text{att}} < P_{\text{def}}$), the attack fails by definition. A failed attack results in no changes. When attack is successful, the defending cell is annexed by the attacking polity. Annexation can also result in ethnocide, as explained below.

Diffusion of Military Technology. The dynamics of spread of MilTech traits are very simple. At the beginning of the simulation, technological traits in all cells bordering on the steppe are set to 1. Subsequently, these traits diffuse out by the process of local diffusion. At each time step, the model samples all agricultural cells and randomly selects a particular locus. If the value of the trait at this locus is 0, nothing happens. If it is 1, the simulation randomly chooses one of four directions and checks whether the neighbor cell in this direction has the particular technology trait. If not, then the technology trait spreads to the neighbor with probability σ . Thus, the value of σ controls the rate of diffusion of technology traits. Once a technology trait spreads to a cell, it is never lost (unlike ultrasocial traits). Note that technological diffusion is exogenous to other processes in the model (it is not affected by warfare or ethnocide). It is essentially a pacesetter determining how fast intense forms of warfare spread from the steppe interface to the rest of Afroeurasia.

Sociocultural Evolution. The dynamics of ultrasociality traits are governed by two processes: local cultural shift (mutation) and ethnocide. A cultural shift process operates as follows: at each time step, 0-valued ultrasociality traits change to 1-valued traits with probability μ_{01} , and 1-valued traits change to 0-valued ones with probability μ_{10} . The assumption of the model is that ultrasociality traits (1s) are greatly disadvantaged, compared with non-ultrasociality traits (0s); we model this simply by assuming that $\mu_{01} \ll \mu_{10}$. Thus, if only the local cultural shift process was operating, ultrasociality traits would be present at a very low level. More precisely, at the equilibrium, the average proportion of loci having 1s is

$$\bar{U} = \frac{\mu_{01}}{\mu_{01} + \mu_{10}}$$

Ethnocide can occur when a defeated cell is annexed by the winning polity. The probability of ethnocide is increased by the number of MilTech traits

possessed by the attacker and decreased by the mountainous terrain (elevation) of the defender:

$$P_{\text{ethnocide}} = \varepsilon_{\min} + (\varepsilon_{\max} - \varepsilon_{\min}) \bar{M}_{\text{att}} - \gamma_1 E_{\text{def}},$$

where \bar{M}_{att} is the sum of technology trait values in the attacking cell divided by n_{mil} (thus, this quantity varies between 0 and 1), and E_{def} is the elevation of the defending cell. Parameter ε_{\min} specifies the probability of ethnocide in the situation when the attacker possesses none of the technology traits, and ε_{\max} the probability when the attacker has all technology traits, assuming that the defender cell is a flatland (elevation = 0). Parameter γ_1 measures the effect of elevation on decreasing the probability of ethnocide. If $P_{\text{ethnocide}} < 0$, nothing happens. If ethnocide occurs, then the values of the ultrasociality vector in the losing cell are set to the values of the attacking cell. Note that this copying process does not directly favor ultrasociality traits (1s). Both 0s and 1s in the winning cell's vector are copied. However, warfare benefits ultrasocial traits indirectly, because polities with more ultrasociality traits have a greater chance of defeating polities with fewer such traits and spreading their traits via ethnocide.

Polity Disintegration. Historical processes of social evolution involved scaling-up dynamics, resulting in larger and more complex societies, and scaling-down dynamics, resulting in social dissolution. The model handles disintegrative process in a highly parsimonious manner. Every time-step, each polity can dissolve into the constituent communities with the probability P_{dissint} . Probability of disintegration increases with the polity size (S) and decreases with the average complexity level (\bar{U}):

$$P_{\text{dissint}} = \delta_0 + \delta_S S - \delta_a \bar{U}.$$

The probability of disintegration is constrained to be between 0 and 1.

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- Campbell DT (1983) The two distinct routes beyond kin selection to ultrasociality: Implications for the humanities and social sciences. *The Nature of Prosocial Development: Theories and Strategies*, ed Bridgeman D (Academic, New York), pp 11–39.
- Richerson PJ, Boyd R (1998) The evolution of human ultrasociality. *Ethnic Conflict and Indoctrination*, eds Eibl-Eibesfeldt I, Salter FK (Berghahn, Oxford), pp 71–95.
- Bowles S (2004) *Microeconomics: Behavior, Institutions, and Evolution* (Princeton Univ Press, Princeton, NJ).
- Fukuyama F (2011) *The Origins of Political Order: From Prehuman Times to the French Revolution* (Farrar, Straus, and Giroux, New York).
- Richerson P, Henrich J (2012) Tribal social instincts and the cultural evolution of institutions to solve collective action problems. *Clodynamics* 3:38–80.
- Carneiro RL (1970) A theory of the origin of the state: Traditional theories of state origins are considered and rejected in favor of a new ecological hypothesis. *Science* 169(3947):733–738.
- Flannery K, Marcus J (2000) *The Evolution Of Human Societies: From Foraging Group to Agrarian State* (Stanford Univ Press, Stanford, CA), 2nd Ed.
- Spencer CS, Redmond EM (2004) Primary state formation in Mesoamerica. *Annu Rev Anthropol* 33:179–199.
- Wright HT (2006) Early state dynamics as political experiment. *J Anthropol Res* 62:305–319.
- Flannery K, Marcus J (2012) *The Creation of Inequality: How Our Prehistoric Ancestors Set the Stage for Monarchy, Slavery, and Empire* (Harvard Univ Press, Cambridge, MA).
- Olson M (1965) *The Logic of Collective Action: Public Goods and the Theory of Groups* (Harvard Univ Press, Cambridge, MA).
- Henrich N, Henrich J (2007) *Why Humans Cooperate: A Cultural and Evolutionary Explanation* (Oxford Univ Press, New York).
- Bowles S, Gintis H (2011) *A Cooperative Species: Human Reciprocity and Its Evolution* (Princeton Univ Press, Princeton, NJ).
- Turchin P (2013) The puzzle of human ultrasociality: How did large-scale complex societies evolve? *Cultural Evolution*, Strüngmann Forum Report, eds Richerson PJ, Christiansen MH (MIT Press, Cambridge, MA), Vol 12, pp 61–73.
- Mann M (1986) *The Sources of Social Power. I. A History of Power from the Beginning to A.D. 1760* (Cambridge Univ Press, Cambridge, UK).
- Bellah RN (2011) *Religion in Human Evolution: From the Paleolithic to the Axial Age* (Harvard Univ Press, Cambridge, MA).
- Wilson DS, Wilson EO (2007) Rethinking the theoretical foundation of sociobiology. *Q Rev Biol* 82(4):327–348.
- Wilson DS (2002) *Darwin's Cathedral: Evolution, Religion, and the Nature of Society* (Univ of Chicago Press, Chicago).
- Bowles S (2009) Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? *Science* 324(5932):1293–1298.
- Henrich J, et al. (2010) Markets, religion, community size, and the evolution of fairness and punishment. *Science* 327(5972):1480–1484.
- Chase K (2003) *Firearms: A Global History to 1700* (Cambridge Univ Press, Cambridge, UK).
- Turchin P (2003) *Historical Dynamics: Why States Rise and Fall* (Princeton Univ Press, Princeton, NJ).
- Lieberman V (2010) *Strange Parallels: Southeast Asia in Global Context, c. 800–1830. Volume II: Mainland Mirrors, Europe, China, South Asia, and the Islands* (Cambridge Univ Press, Cambridge, UK).
- Levy JS, Thompson WR (2011) *The Arc of War: Origins, Escalation, and Transformation* (Univ of Chicago Press, Chicago).
- Turchin P (2009) A theory for formation of large empires. *J Global Hist* 4:191–207.
- Gat A (2008) *War in Human Civilization* (Oxford Univ Press, New York).
- Gavrilets S, Anderson D, Turchin P (2010) Cycling in the complexity of early societies. *Clodynamics* 1:58–80.
- Scott JC (2009) *The Art of Not Being Governed: An Anarchist History of Upland Southeast Asia* (Yale Univ Press, New Haven, CT).
- Michaud J (2010) Zomia and beyond. *J Global Hist* 5:187–214.
- Christian D (1998) *A History of Russia, Central Asia, and Mongolia* (Blackwell, Oxford).
- Dormann CF, et al. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography* 30:609–628.
- Bockstette V, Chanda A, Putterman L (2002) States and markets: The advantage of an early start. *J Econ Growth* 7:347–369.
- Toynbee AJ (1957) *A Study of History* (Oxford Univ Press, London), Vol 2.
- Diamond J (1997) *Guns, Germs, and Steel: The Fates of Human Societies* (Norton, New York).
- Turchin P (2008) Arise 'clodynamics' *Nature* 454(7200):34–35.
- Currie TE, Greenhill SJ, Gray RD, Hasegawa T, Mace R (2010) Rise and fall of political complexity in island South-East Asia and the Pacific. *Nature* 467(7317):801–804.
- Nefedov SA (2009) *War and Society* (Territoriya Buduschego, Moscow). Russian.