

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

Peter Turchin<sup>a,1</sup>, Thomas E. Currie<sup>b</sup>, Edward A. L. Turner<sup>c</sup>, and Sergey Gavrilets<sup>d</sup>

<sup>a</sup>Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06235-3042; <sup>b</sup>Centre for Ecology and Conservation, Department of Biosciences, University of Exeter, Cornwall TR10 9EZ, United Kingdom; <sup>c</sup>South Woodham Ferrers, CM3 5GU, England; and <sup>d</sup>Department of Ecology and Evolutionary Biology and Department of Mathematics, National Institute for Mathematical and Biological Synthesis, University of Tennessee, Knoxville, TN 37996

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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.**

Author contributions: P.T., T.E.C., and S.G. designed research; P.T., T.E.C., E.A.L.T., and S.G. performed research; P.T. and T.E.C. analyzed data; and P.T., T.E.C., and S.G. wrote the paper.

The authors declare no conflict of interest.

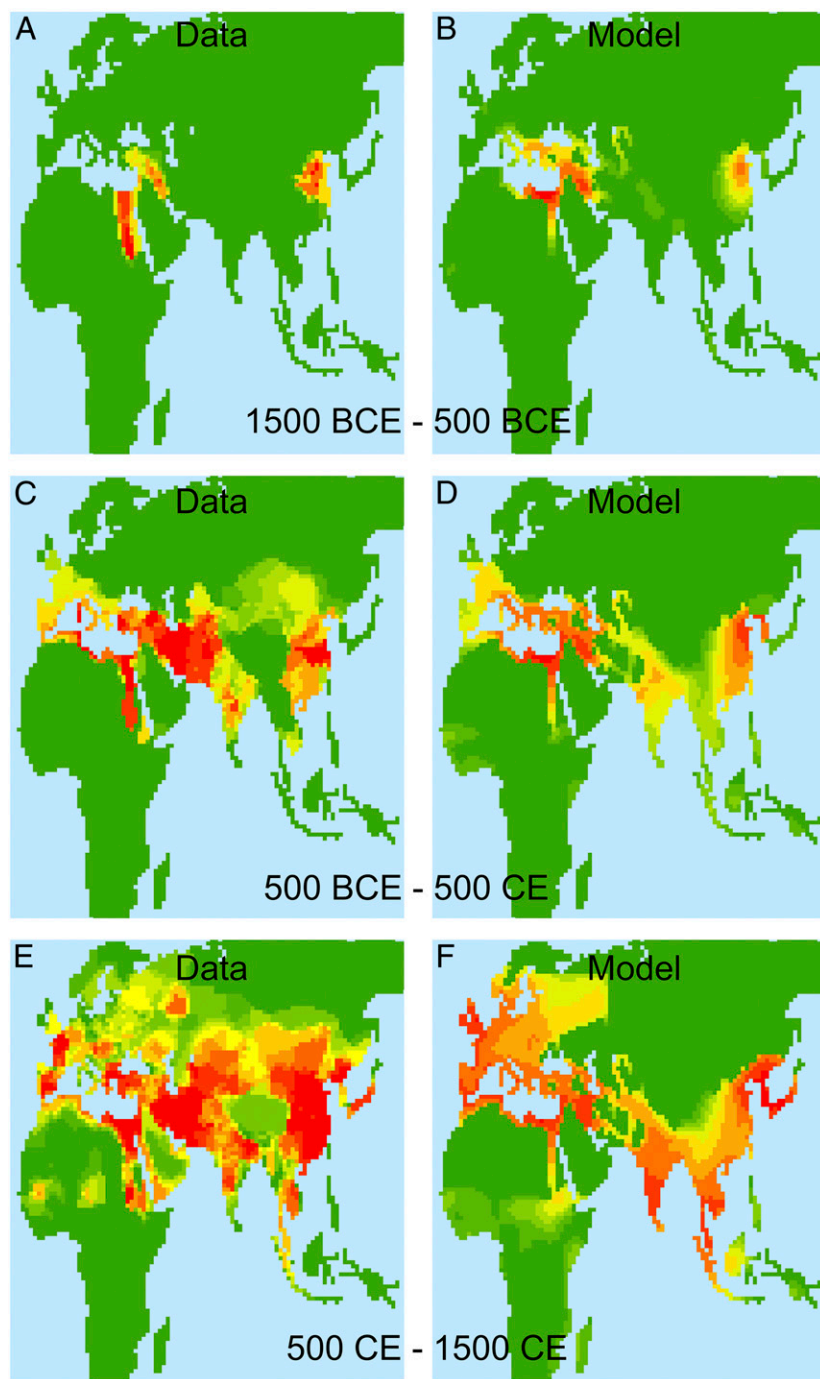
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<sup>1</sup>To whom correspondence should be addressed. E-mail: peter.turchin@uconn.edu.

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**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.

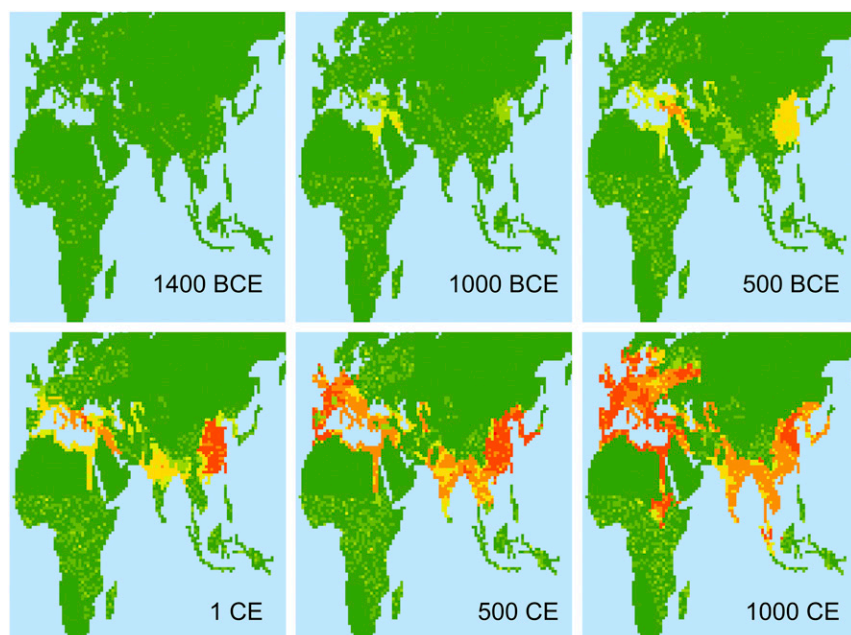
The importance of the steppe frontier in the evolution of ultrasociality is supported by spatially explicit statistical analyses of imperial density maps. Simultaneous autoregressive models (SAR), which account for spatial autocorrelations in the data

(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



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  $\sigma$ . Thus, the value of  $\sigma$  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  $\mu_{01}$ , and 1-valued traits change to 0-valued ones with probability  $\mu_{10}$ . 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  $\bar{M}_{\text{att}}$  is the sum of technology trait values in the attacking cell divided by  $n_{\text{mil}}$  (thus, this quantity varies between 0 and 1), and  $E_{\text{def}}$  is the elevation of the defending cell. Parameter  $\varepsilon_{\min}$  specifies the probability of ethnocide in the situation when the attacker possesses none of the technology traits, and  $\varepsilon_{\max}$  the probability when the attacker has all technology traits, assuming that the defender cell is a flatland (elevation = 0). Parameter  $\gamma_1$  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  $P_{\text{disint}}$ . Probability of disintegration increases with the polity size ( $S$ ) and decreases with the average complexity level ( $\bar{U}$ ):

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

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

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# Supporting Information

## War and Space: Explaining the Evolution of Old World Complex Societies

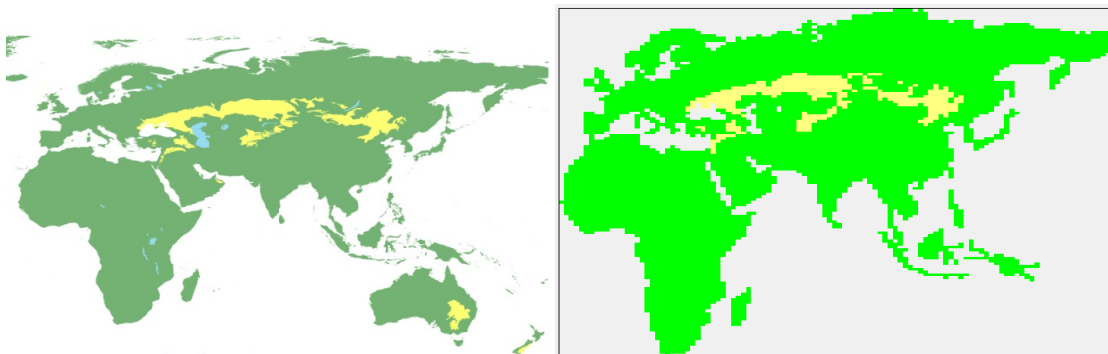
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### I. Model Description

#### I.1 The modeled period, area, and spatial units

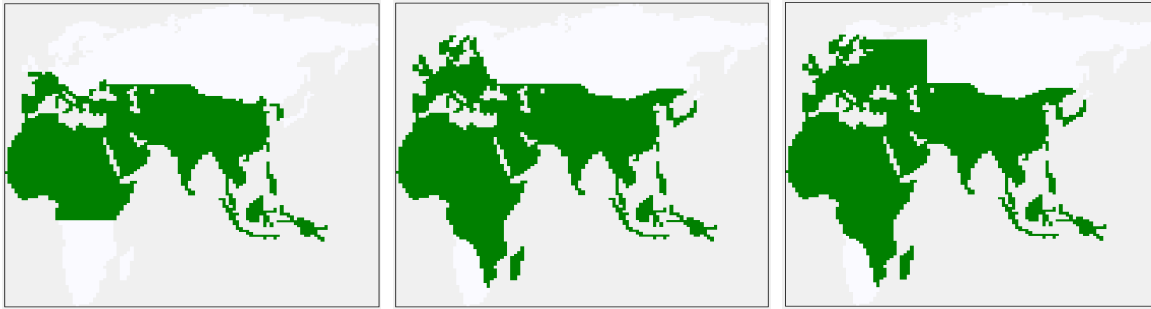
The model simulates social evolution during the period between 1500 BCE and 1500 CE. All modeled interactions take place within a two-dimensional rectangular grid of cells, each representing a  $100 \text{ km} \times 100 \text{ km}$  square of the Earth's surface. This grid was created in ArcGIS v9.3 using Hawth's Analysis Tools (Beyer 2004) under a conic equidistant projection. The modeled area includes Eurasia and Africa (the 'Old World'). Each cell is classified as either sea or land. Land cells are characterized by average elevation, and are further classified into desert, steppe, or agriculture categories. Agricultural cells are non-desert and non-steppe areas to which agriculture has spread during the current period (thus, the extent of the area where agriculture is practiced expands during the simulation). Additionally, as explained above, desert cells through which major rivers flow are treated as agricultural cells.

Assessment of the extent of the Eurasian Steppe was made according to the World Wildlife Fund's (WWF) global map of terrestrial ecosystems(1). The biome labeled, "*Temperate grasslands, savannas, and shrublands (temperate, semiarid)*" was used to designate grid cells as being Steppe or not (see figure S1). These vast grasslands run almost contiguously from Northeastern China, through Asia and Europe to the Black Sea and down into the region of Syria and even some places in Turkey. A small region in the Eastern part of the Arabian Peninsula also belongs to this biome. However, this is far removed from the other grasslands and was not involved in the historical development and spread of horse-based military technology that we focus on in this paper, and is therefore not designated as steppe in our simulations. The mean distance to the Steppe (in kilometers) was also calculated for use in spatially explicit statistical analyses (see below). The grid was overlaid on high resolution climate maps (resolution  $\sim 1 \text{ km}^2$ ),(2) in order to assess precipitation, and topography. Cells were classified as 'desert' and therefore non-agricultural if their mean annual rainfall was less than 250 mm. For each cell the mean elevation (in meters) was calculated.



**Figure S1.** Classification of the Steppe in our simulation (right) is based on the WWF map of terrestrial ecosystems (left). The grassland regions in Eastern Arabia, are not classified as Steppe for the purposes of this model, and those in New Zealand and Australia do not form part of the Afro-Eurasian region we focus on in this paper. Steppe regions are shown in yellow in both figures.

Our map of the extent of agriculture at the beginning of the simulation (1500 BCE), is based on Bellwood (3: figure 0.1), with the following areas excluded: (1) the Bantu expansion over subequatorial Africa, which probably occurred sometime after 500 BCE; and (2) Japan, again after 500 BCE. Additionally, we have taken into account the *terrestrial plant threshold* (TPT) occurring at Effective Temperatures of 12.75°C (4: Table 4.02 and figure 4.12). The TPT marks the northern boundary of the area where plant productivity is sufficiently high to permit plant-dominated subsistence strategies by hunter-gatherers. This is also the area where intensification of production leads to the domestication and diffusion of plant cultivars (5). When plants were first domesticated (in regions south of the isotherm) they spread readily West and East (6). The northward spread, especially across the TPT, was much slower and required a lengthy period of adaptation to colder climates. For example, Bronze Age populations in the European forest belt north of the TPT practiced agropastoralism with a heavy emphasis on animal-dominated strategies (7). Productive agriculture, capable of sustaining complex societies, appeared in Northern and later Eastern Europe only during the first millennium CE. Thus, the extent of agriculture, and therefore the modeled area increases throughout the simulation (see below for details, Figure S2).



**Figure S2.** The extent of agriculture in the simulation (green) increases throughout the simulation (earliest period, left; final period, right)

Only agricultural cells are explicitly modeled. Each agricultural cell is occupied by a ‘community.’ Each community is characterized by two binary vectors of cultural traits. The first one,  $U$ , contains  $n_{\text{ultra}}$  “ultrasociality traits” and the second one,  $M$ , contains  $n_{\text{mil}}$  of military technology (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 which, 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’), while MilTech traits change by diffusion. These processes are described in greater detail below.

## I.2 Model parameters: estimating initial values

Model parameters were estimated in a two-stage process. In the first stage, we came up with a parameter ‘reference set’ using a variety of *a priori* reasoning. The purpose of this exercise was to arrive not at precise values of parameters, but to estimate their orders of magnitude. In the second phase, we used the



direct grid search approach to explore the parameter space. Again, our goal was not to obtain point estimates (we are not interested in parameter values *per se*), but to locate the region within the parameter space for which the model dynamics exhibits a good fit with the data. Here we describe the logic underlying initial estimates of parameters, and in Section III.1 we provide details of the search of the parameter space.

The time step in the model was set to 2 years. Thus, the duration of the simulation was 1500 steps (or 3,000 years, corresponding to the period from 1500 BCE to 1500 CE).

The number of ultrasocial traits was set to 10, and MilTech traits to 5. The probability of a MilTech diffusing to a nearby cell without one was 0.25 per time step. This diffusion rate was chosen so that MilTech traits would diffuse throughout the simulated area by the end of simulation.

As explained above, at the start of simulation (1500 BCE) only cells within the set Agri1 are allowed to build multicell polities by attacking and annexing other agricultural cells. We also assume that by the second half of the first millennium agriculture has spread to all cells within Agri3. In the simulation this occurs at time step = 1100 (corresponding to 700 CE). The timing of agriculture spread to cells within Agri2 is earlier, but it is unclear when this happened. We estimated the onset of Agri2 empirically, by running the model for the value of this parameter equal to 100, 200, ... 1000. The value that yielded the highest  $R^2$  (the coefficient of determination) for the fit of model predictions to data was 900 (300 CE), and this is the value that we used.

Parameter  $\beta$  measures the effect of the product of average ultrasociality and the size (number of cells) of the polity on its military power. This parameter was set to 1. The related parameter  $\gamma$  translates elevation of the defending cell (in km) into its defensive power. This parameter was set to 4, so that 1,000 m of elevation in a mountainous cell with no ultrasocial traits makes its power the same as a plains cell with four ultrasocial traits.

Parameters regulating ethnocide were set as follows. The maximum probability of ethnocide,  $\varepsilon_{\max}$ , was set to 1, and the baseline probability  $\varepsilon_{\min}$  was  $1/20^{\text{th}}$  of it, or 0.05. The effect of elevation,  $\gamma_1$ , was set to 1.

Baseline disintegration probability  $\delta_0$  was set to 0.05, which corresponds to the assumption that even smaller polities with a lot of ultrasocial traits collapse on average every 20 time steps (or 40 years, corresponding to 2 ruler generations). Parameter  $\delta_s$  was also set to 0.05. Thus, a polity without any ultrasocial traits collapses with probability = 1 when it reaches the size of 19 cells. Parameter  $\delta_a$  was set to 2. This means that each additional unit of average ultrasociality extends the threshold size by  $2/0.05 = 40$  cells. Thus, even with all ultrasocial traits present polities cannot exceed the size of approx. 400 cells without collapsing.

Parameters setting mutation rates were  $\mu_{01} = 0.0001$  and  $\mu_{10} = 0.002$ . Thus, at the mutation equilibrium the frequency of ultrasocial traits is less than 0.05.

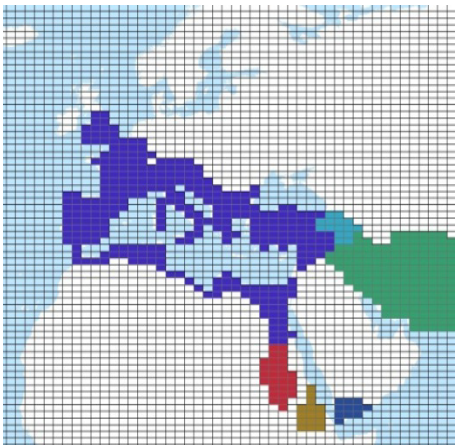
Finally, the distance of sea-based attack,  $d_{\text{sea}}$ , was set to 1 at the beginning of the simulation and then was incremented by  $\Delta = 0.025$  every time step. Model parameters are summarized in Table SM1.

**Table SM1.** Model parameters.

<i>Parameter</i>	<i>Reference value</i>	<i>Explanation</i>
$\beta$	1	effect of average ultrasociality on power
$\varepsilon_{\min}$	0.05	minimum probability of ethnocide (with all MilTech = 0)
$\varepsilon_{\max}$	1	maximum probability of ethnocide (with all MilTech = 1)
$\delta_0$	0.05	baseline probability of disintegration (for $S = 0$ and $U = 0$ )
$\delta_s$	0.05	effect of polity size on probability of disintegration
$\delta_a$	2	effect of average ultrasociality on probability of disintegration
$\mu_{01}$	0.0001	probability of mutation to an ultrasocial trait
$\mu_{10}$	0.002	probability of ultrasocial trait mutating to non-ultrasocial trait
$\gamma$	4	effect of elevation on defensive power
$\gamma_1$	1	effect of elevation on the probability of ethnocide

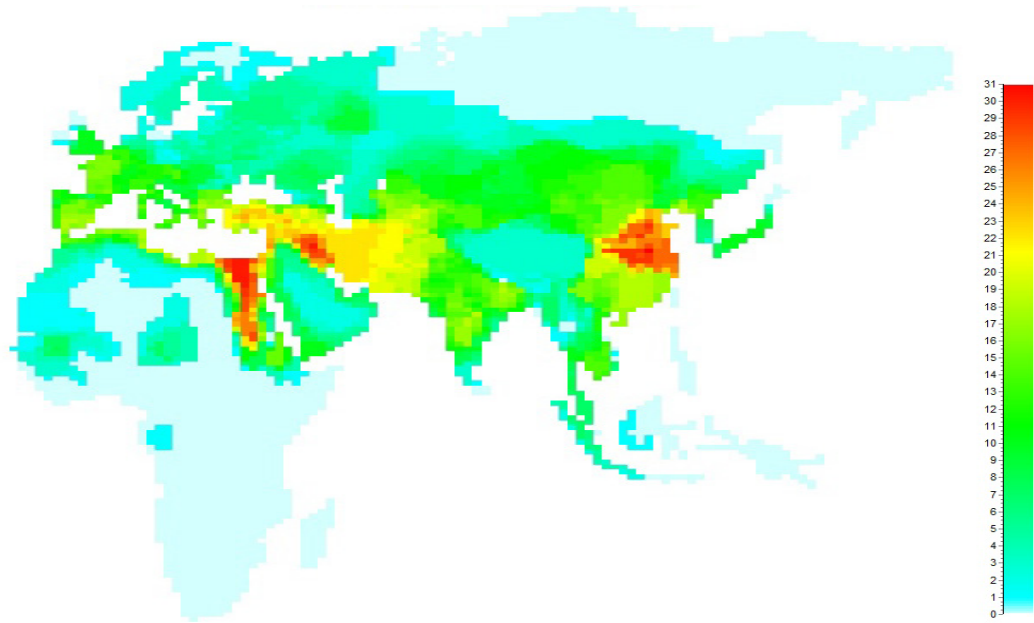
## II. Estimation of Imperial Density Maps from Historical Data

In order to test the simulation model, data were collected on the distributions of large-scale polities during the time frame 1500 BCE to 1500 CE in the Afro-Eurasia region described above. One of us (E.T.) used a variety of historical atlases and other sources (see below) to create hand-drawn reference maps of the geographic distribution of large, well-attested polities at 100-year time-steps (1500 BCE, 1400 BCE,..., 1500 CE). Using ArcGIS v9.3 information from these maps were then integrated into a geographical information system (by T.C.) based on the same grid map used for the simulations. As the original maps used to create our reference maps were created in a manner blind to the particular hypothesis being tested here, where possible these original maps were used to determine the boundaries and extent of the polities identified in the reference maps. All these maps were geo-referenced to ensure they were projected in the same way as the grid map. The grid was overlaid on to these maps. For each time slice, if a polity covered 10 or more grid cells (Figure S3 gives an example of one such time slice), then this polity was entered into our database and the appropriate grid cells were indicated as belonging to this polity. Obviously, the borders of a polity rarely coincide exactly with the rigid, straight lines of our grid cells. Therefore a grid cell was assigned to a particular polity if that covered approximately 50% or more of the grid cell.



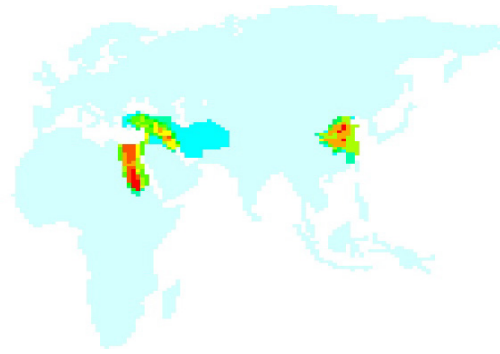
**Figure S3.** Estimated distributions of the Roman Empire (blue) and other large-scale polities from one time slice.

Therefore for each cell we have a record of the number of time steps in which that cell was inhabited by a polity large enough to meet the cut-off criteria. This enabled the construction of an imperial density map for the entire time period showing the regions in which large polities occurred more often (Figure S4). To assess the time dynamics of polity distributions we calculated imperial densities for each thousand-year period (this relates to the following time slice maps (A) 1500 BCE - 400 BCE, (B) 500 BCE - 400 CE, and (C) 500 CE - 1500 CE (Figure S5).

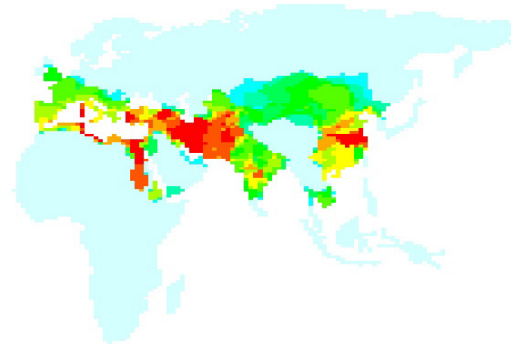


**Figure S4.** Imperial Density Map 1500 BCE – 1500 CE. Scale shows how many time slices polities were present in each cell. Red cells indicate regions that were more frequently inhabited by large-scale polities. Cyan cells show where large polities were less common. The lightest blue regions indicate the absence of large polities during the time-span considered in this paper.

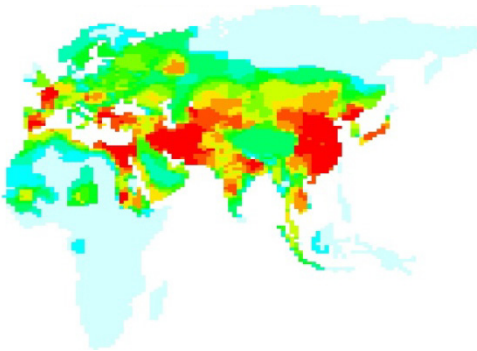




(A)



(B)



(C)

**Figure S5.** Imperial Density Maps for (A) 1500 BCE - 400 BCE, (B) 500 BCE - 400 CE, and (C) 500 CE - 1500 CE.

***References used for creating Imperial Density Maps:***

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### III. Supplementary Results

#### III.1 Exploration of the Parameter Space

Imperial density data,  $Z(x,y,t)$ , is the frequency (measured with a century step) with which a cell at spatial coordinates  $x,y$  finds itself in a polity with territory greater than 10 grid cells during era  $t$ . In comparisons with model predictions we only look at the set of spatial coordinates of cells with agriculture,  $\{x,y\} \in \text{AGRI}$ . Era  $t = 1, 2, 3$  refers to (1) 1500–500 BCE, (2) 500 BCE–500 CE, or (3) 500–1500 CE.

The model is sampled in the same way as data. Thus, the model prediction  $\hat{Z}(x,y,t)$  is the frequency with which a cell at  $x,y$  is found within a multicell polity with 10 cells or more during era  $t$ .

Our measure of model accuracy is the coefficient of determination ( $R^2$ , the proportion of variance explained by the model) in the linear regression of  $Z$  on  $\hat{Z}$ . We calculate both the overall  $R^2$  for all three eras, and  $R^2$  for each era separately, to determine in which eras the model performs better at explaining the observed empirical patterns. In explorations of parameter space we used as the objective function the overall  $R^2$  that tells us how well the model captures both the spatial and temporal dynamics of macrostate incidence in the historical record (the era-specific  $R^2$  capture spatial, but not temporal variation in the data). There was a substantial variation between different realizations of the model, which resulted in coefficients of determination changing by 0.02–0.03 between different runs. Experimentation showed that by averaging  $\hat{Z}$  over 5 replicates the estimate of  $R^2$  can be stabilized to within 0.01. Accordingly, during

parameter explorations we replicated each parameter combination 5 times. For key results (the reference set, the ‘best set’, etc.) we used 20 replicates.

Figure S6 shows the comparison between the data (left column) and model predictions for the reference set of parameters. During Era 1 the model predicts the same three ‘imperiogenesis hotspots’ (in Mesopotamia, Egypt, and North China) as in data, although within these three regions the actual distributions of macrostate incidence are not well captured. In Era 2 the model correctly captures the spread of large-scale societies into the central Mediterranean/Western Europe, North India, South China, and the beginnings of state formation in continental Southeast Asia. The model misses nomadic polities northwest of China because it only simulates agrarian societies. Additionally, the model does not predict the observed dense concentration of macrostates in Iran, because most of the Iranian plateau is desert, and the model assumes that desert cells cannot support complex societies. Finally, in Era 3 the model predicts the spread to northern and eastern Europe, Japan, and southeast Asia, matching the empirical pattern.

The match between model predictions and data calculated separately for each era is  $R^2 = 0.54$ , 0.35, and 0.34, while the overall  $R^2 = 0.47$ . One obvious reason for a relatively poor model performance for Era II is the predicted spread of macrostates into Northern Europe, which anticipates the actual rise of complex societies there by a thousand years. A grid search over possible values of  $\tau_2$  indicated that increasing the value of this parameter from 500 to 900 dramatically improves the fit for Era 2, raising  $R^2$  from 0.35 to 0.52 (Figure S7), and overall  $R^2$  to 0.51.

Next we investigate how sensitive model performance is to specific values of parameters by varying each parameter, in turn, from a value one-half to double the reference values (Table SM2). The results show that the model is not unduly sensitive to any parameter. For about half of them the coefficient of determination hardly changes, and for all values of parameters  $R^2$  stays within relatively narrow bounds, 0.41–0.56. In other words, the model explains roughly one-half of variance in the data for a broad band of parameter values around the reference set.

The grid search of the parameter space indicated that an improvement of the overall  $R^2$  to 0.65 can be achieved by changing the values of only three parameters,  $\varepsilon_{\max}$ ,  $\delta_0$ , and  $\gamma$  (in addition to  $\tau_2$  that we have fitted in the first step). This ‘best parameter set’ also improves the degree of fit as judged by visual inspection of data and model-predicted patterns (Figure S8). Again, the close match between the observed and predicted values is relatively insensitive to the variation in model parameters (Table SM3).

**Table SM2.** Results of varying model parameter on the match between model predictions and data, measured by prediction  $R^2$ . The simulation was run by varying each parameter in turn, by multiplying its reference value with the ‘factor’ (0.5, 0.75, ... 2). This exploration is centered on the reference set estimates with  $\tau_2 = 900$ .

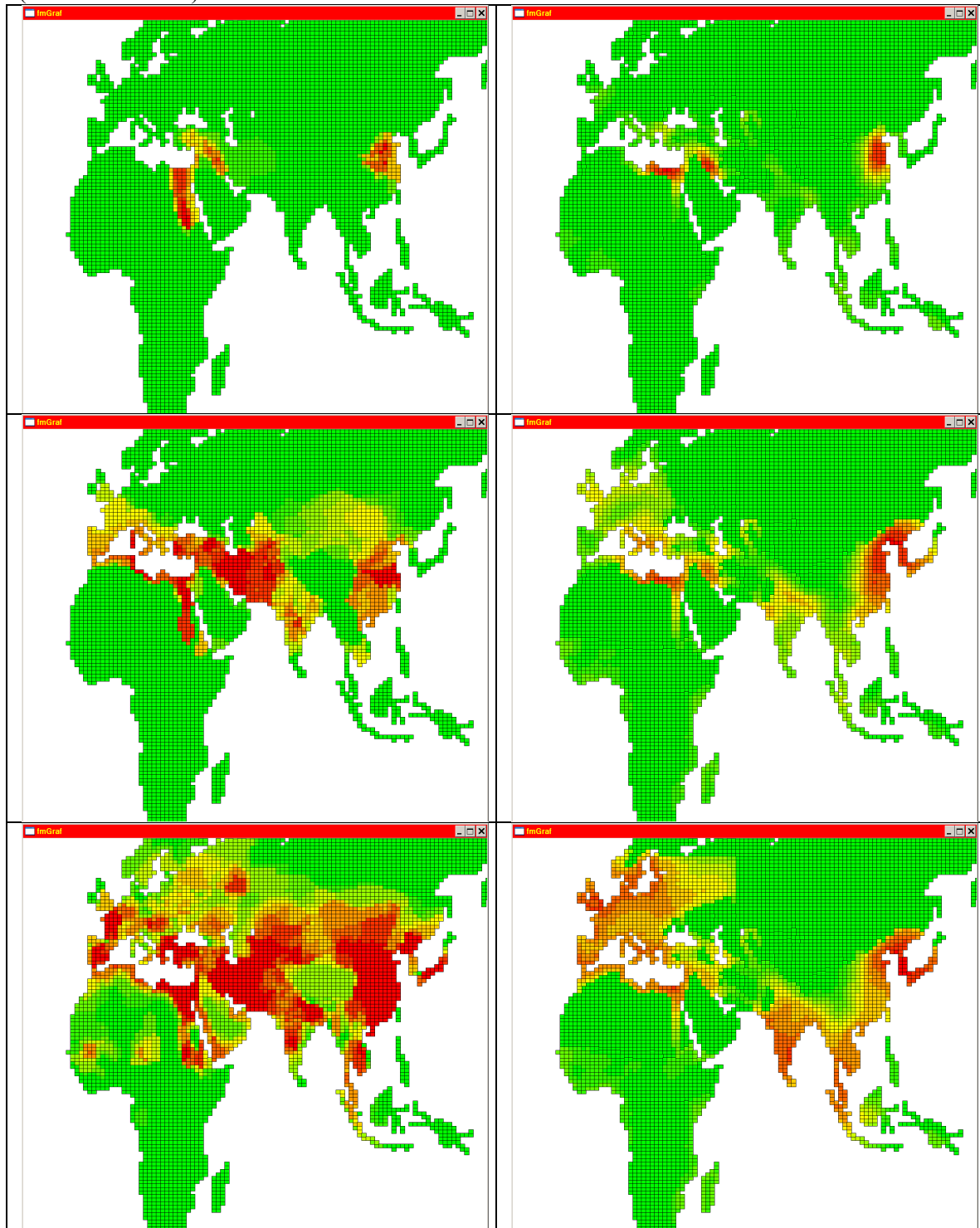
Parameter	Factors				
	0.5	0.75	1	1.5	2
$\beta$	0.42	0.48	0.51	0.54	0.56
$\varepsilon_{\min}$	0.51	0.52	0.51	0.51	0.50
$\varepsilon_{\max}$	0.41	0.48	0.51	0.56	0.56
$\delta_0$	0.54	0.52	0.51	0.49	0.45
$\delta_s$	0.54	0.52	0.51	0.49	0.47
$\delta_a$	0.48	0.51	0.51	0.52	0.54
$\mu_{01}$	0.47	0.50	0.51	0.50	0.49
$\mu_{10}$	0.49	0.50	0.51	0.52	0.50
$\gamma$	0.56	0.53	0.51	0.44	0.45
$\gamma_1$	0.54	0.52	0.51	0.48	0.44



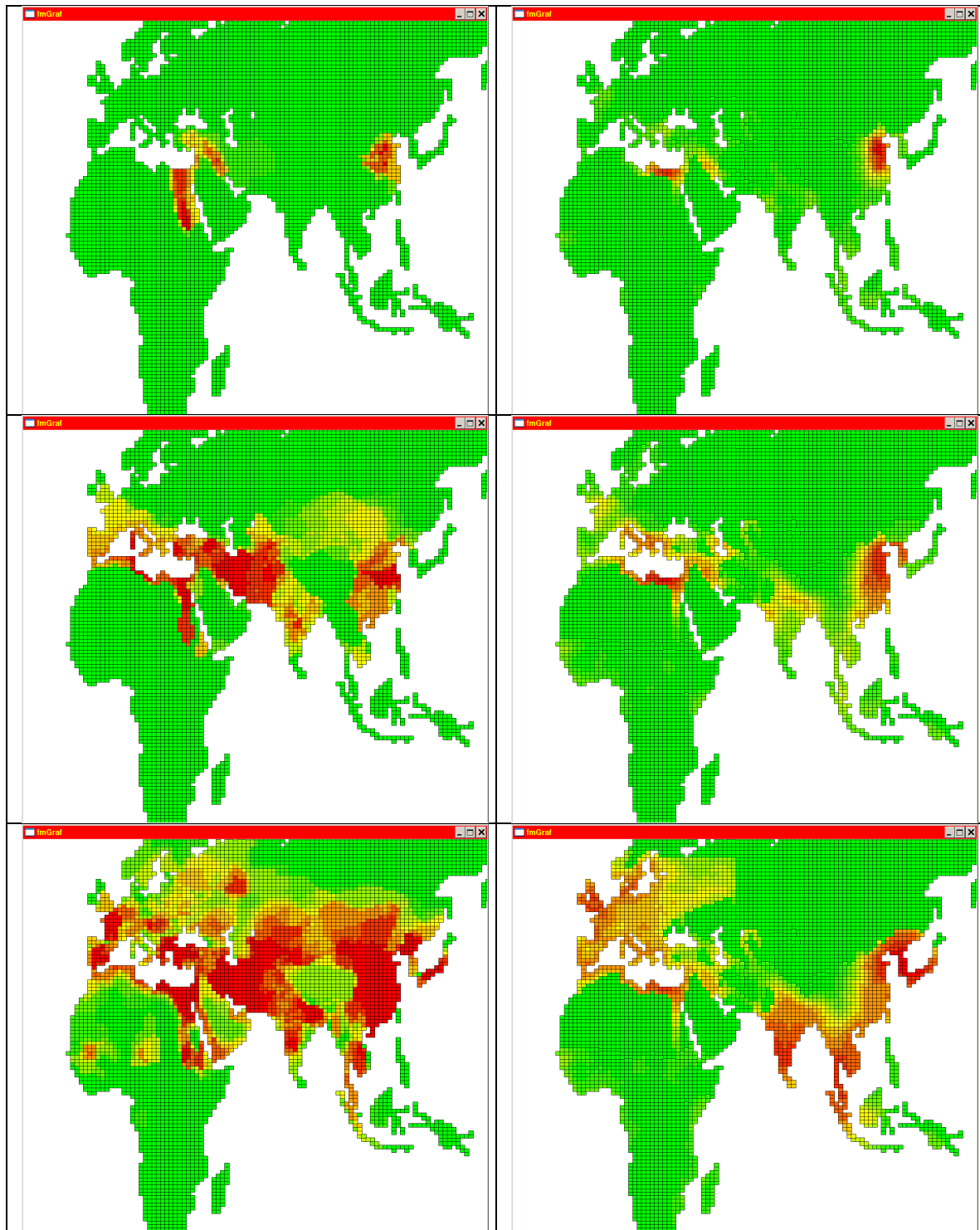
**Table SM3.** Results of varying model parameter on the match between model predictions and data, measured by prediction  $R^2$ . The simulation was run by varying each parameter in turn, by multiplying its reference value with the ‘factor’ (0.5, 0.75, ... 2). This exploration was centered on the ‘best’ estimates of parameters.

Parameter	Factors				
	0.5	0.75	1	1.5	2
$B$	0.61	0.62	0.65	0.65	0.64
$\varepsilon_{\min}$	0.64	0.65	0.65	0.64	0.63
$\varepsilon_{\max}$	0.59	0.63	0.65	0.63	0.63
$\delta_0$	0.65	0.64	0.65	0.63	0.62
$\delta_s$	0.60	0.64	0.65	0.64	0.64
$\delta_a$	0.64	0.63	0.65	0.63	0.62
$\mu_{01}$	0.64	0.65	0.65	0.61	0.56
$\mu_{10}$	0.60	0.64	0.65	0.65	0.65
$\Gamma$	0.67	0.65	0.65	0.63	0.60
$\gamma_1$	0.63	0.64	0.65	0.63	0.60
$d_{\text{sea}}$	0.64	0.65	0.65	0.62	0.62
$\Delta$	0.66	0.65	0.65	0.62	0.59

**Figure S6.** Comparison between data (left column) and model (right column) for three historical eras (top: 1500–500 BCE, middle: 500 BCE–500 CE; bottom: 500–1500 CE). Reference parameter set (overall  $R^2 = 0.47$ ).

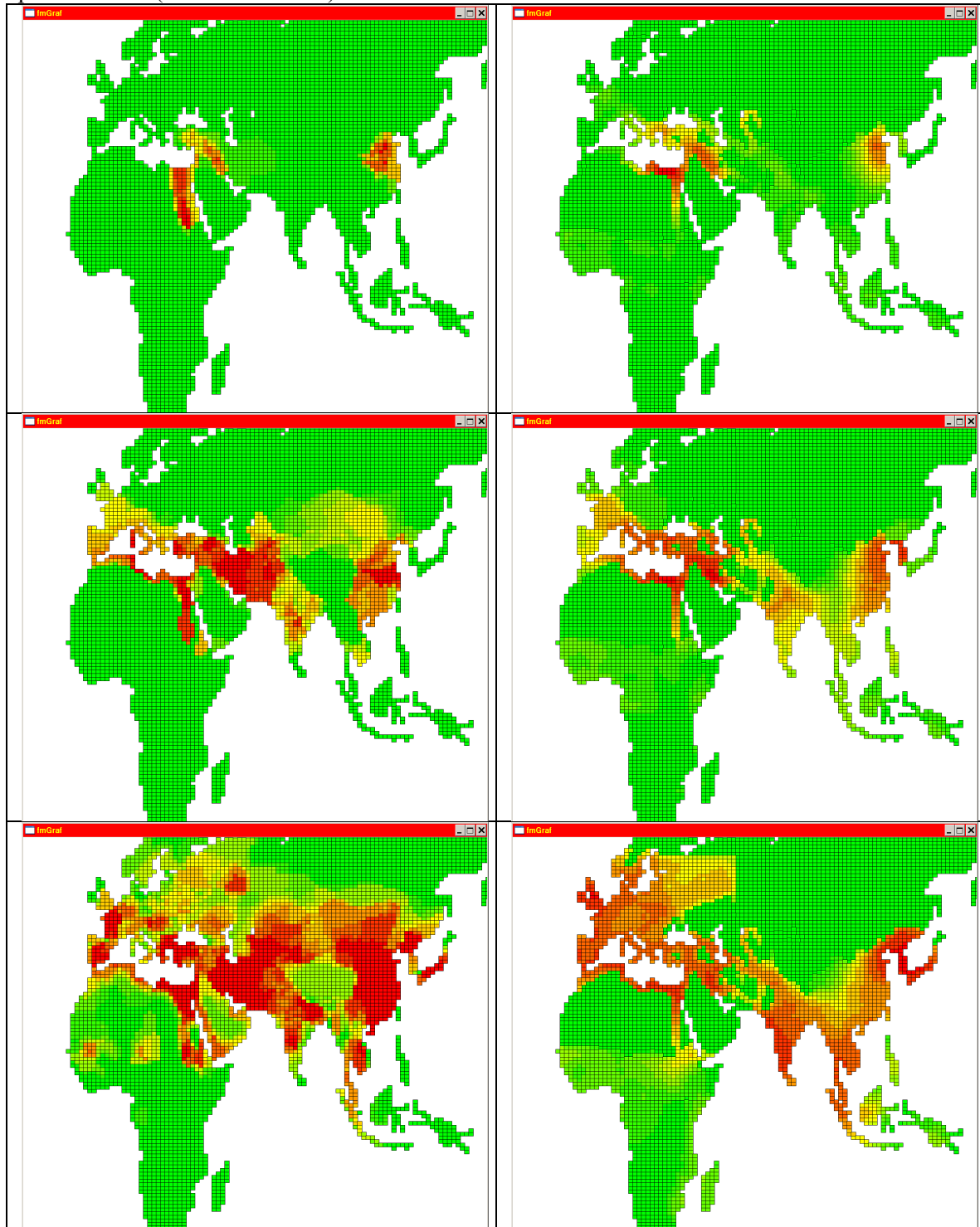


**Figure S7.** Comparison between data (left column) and model (right column) for three historical eras (top: 1500–500 BCE, middle: 500 BCE–500 CE; bottom: 500–1500 CE). Reference parameter set with  $\tau_2 = 900$  (overall  $R^2 = 0.51$ ).





**Figure S8.** Comparison between data (left column) and model (right column) for three eras. Best parameter set (overall  $R^2 = 0.65$ ).



### III.2 Null Models: Effects of Turning off CMLS and Elevation

The observation that model performance (ability to predict spatio-temporal distribution of imperial density) is not sensitive to precise values of parameters raises the question of what will happen if we selectively turn off certain structural components of the model. This allows us to assess whether alternative, simpler processes could account for the observed data. For example, the match between the simulated data and the empirical data could be due to the particular shape of the grid (reflecting the geography of the old world landmass) on which we are running the model.

The conceptual core of the model is the effect of MilTech traits on the intensity of cultural multilevel selection (CMLS). We can eliminate the influence of MilTech on the probability of ethnocide by setting parameters  $\varepsilon_{\min}$  and  $\varepsilon_{\max}$  to the same value. Running the model for several values of  $\varepsilon_{\min}$  and  $\varepsilon_{\max}$  we observe a dramatic reduction in the overall  $R^2$  (Table SM4). Note that warfare between polities and ethnocide in conquered cells are simulated in exactly the same way as in the full model; it is the connection between MilTech and ethnocide that is broken. The MilTech-independent intensity of ethnocide ( $\varepsilon_{\min} = \varepsilon_{\max} = 0.2, 0.5$ , or  $1$ ) has a very slight effect on the results. The somewhat positive values of the overall  $R^2$  ( $0.15$ – $0.17$ ) are probably due to the effect of long-term presence of agriculture (this is supported by the regression analyses in the next section).

Another key assumption of the model is that MilTech traits diffuse out from the Steppe, creating a geographical pattern of variation in the CMLS intensity. We can eliminate the effect of distance from the Steppe on CMLS intensity by seeding initial MilTech traits randomly within agricultural cells, rather than on the Steppe frontier. When MilTech traits are seeded randomly, the results are essentially the same as with breaking the connection between MilTech and ethnocide – most of predictability is lost (Table SM4).

We also investigated the effect of turning off the influence of elevation on defensive power and on the probability of ethnocide. Setting  $\gamma = 0$  (no elevation effect on defensive power) reduces  $R^2$  for the first era, but also results in slightly better predictabilities for Eras 2 and 3, and no change in the overall  $R^2$ . On the other hand, setting  $\gamma_1 = 0$  (no elevation effect on ethnocide) has a measurably negative effect on all  $R^2$ . Setting both  $\gamma$  and  $\gamma_1 = 0$  further decreases the ability of the model to predict data. This exercise suggests that the main effect of elevation in the model is the one mediated by cultural selection on ultrasocial traits.

Finally, eliminating elevation effects in addition to the effect of MilTech on ethnocide results in the same overall  $R^2$  as in the model only lacking MilTech-ethnocide connection (Table SM4).

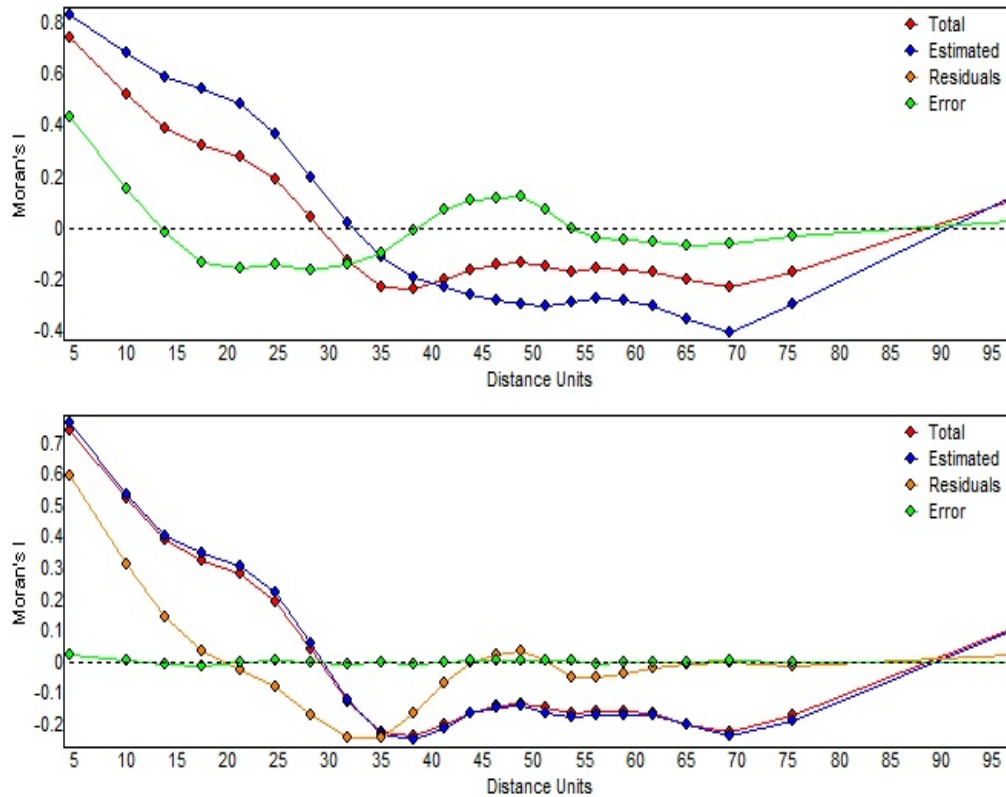
**Table SM4.** Effect of turning off various components of the model on its ability to predict data ( $R^2$  for each era, and overall  $R^2$ ). All results based on 20 replicate model runs.

Model	Era 1	Era 2	Era 3	Overall
Full model	0.56	0.65	0.47	0.65
No elevation effect on defensive power ( $\gamma = 0$ )	0.43	0.68	0.53	0.65
No elevation effect on ethnocide ( $\gamma_1 = 0$ )	0.45	0.59	0.40	0.59
No elevation effects ( $\gamma = \gamma_1 = 0$ )	0.31	0.46	0.35	0.48
No effect of MilTech on ethnocide ( $\varepsilon_{\min} = \varepsilon_{\max} = 0.2$ )	0.09	0.10	0.02	0.17
No effect of MilTech on ethnocide ( $\varepsilon_{\min} = \varepsilon_{\max} = 0.5$ )	0.08	0.08	0.02	0.16
No effect of MilTech on ethnocide ( $\varepsilon_{\min} = \varepsilon_{\max} = 1$ )	0.04	0.10	0.00	0.15
No effect of the Steppe (MilTech seeded randomly)	0.03	0.11	0.00	0.17
Null model (no effects of MilTech* and elevation)	0.04	0.17	0.00	0.16

\*  $\varepsilon_{\min} = \varepsilon_{\max} = 0.5$

### III.3 Spatially-Explicit Regression Analyses

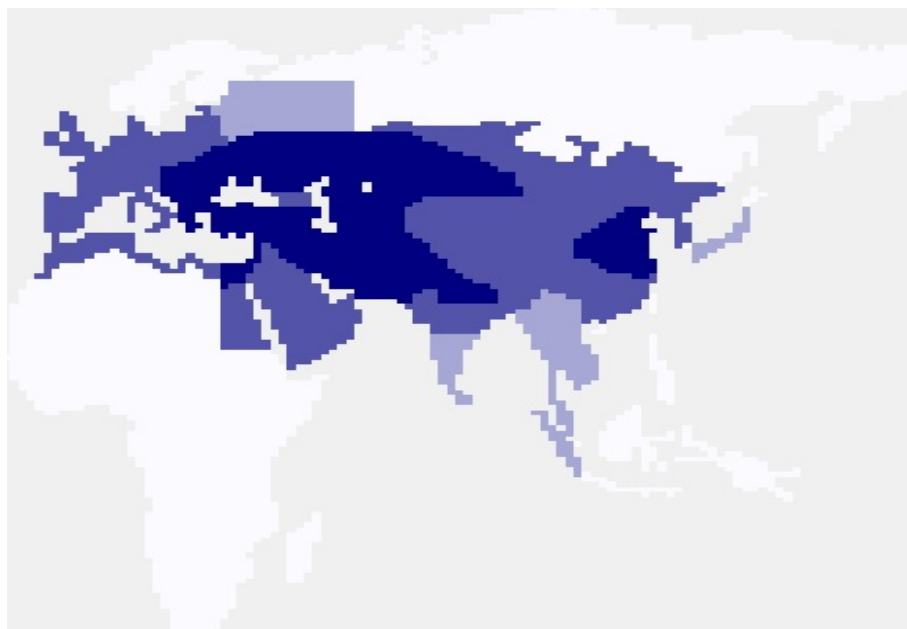
To complement the results of the simulation model we performed statistical analyses of the data on the historical distribution of empires. We examined the effect of the same ecological and historical factors discussed above as predictors of imperial density. As the data take the form of a grid the data points may show a substantial degree of spatial autocorrelation (Figure S9). The assumptions of standard statistical procedures such as Ordinary Least Squares regression may not hold in cases such as this, running the risk of inaccurate parameter estimation, and inflated type I errors (i.e., falsely rejecting the null hypothesis of no association between the predictor and response variables) (8). To control for spatial autocorrelation in the data we ran a series of Simultaneous Autoregressive Models (SAR) models in the package SAM v4.0 (Spatial Analysis in Macroecology) (9). This approach explicitly models spatial autocorrelation in the residuals with the effects of surrounding cells being weighted according to how far away they are (specifically  $\frac{1}{d^\alpha}$ , where  $d$  is distance). The  $\alpha$  parameter, therefore, affects the extent to which spatial autocorrelation is modeled as occurring. By choosing a suitable value for alpha, spatial autocorrelation in the error term of the model can be removed, and the unique effects of the predictor variables can be assessed. In these analyses initial explorations of the data indicated that value of  $\alpha = 3$  was suitable for effectively reducing spatial autocorrelation in the error term. In all cases the autoregressive parameter,  $\rho$ , was estimated.



**Figure S9.** Moran's I spatial autocorrelation plots at increasing distances (hundreds of kilometers) for total imperial density (red), predicted imperial density from SAR analysis (blue), SAR analysis residuals, reflecting the spatial autocorrelation component of the model (orange), and SAR error term (green). The two plots show models with the same predictor and response variables, but in the top plot no correction has been made for spatial autocorrelation while in the second this correction has been made resulting in an error term that is no longer spatially autocorrelated.



In all analyses the dependent variable is imperial density (number of times cell is inhabited by large polity) over the full time span (1500 BCE – 1500 CE) and is treated as varying continuously for the purposes of these analyses. The cells considered are the same as in the simulation (i.e. only those cells in which agriculture was present at some point). Four predictor variables were examined: (1) the long-term presence of agriculture, (2) distance from the Steppe, (3) elevation, and (4) presence and duration of horse-based warfare. The long-term presence of agriculture indicates whether cells had agriculture at the beginning of our period, 1500 BCE (as opposed to acquiring it at a later date). Distance from the Steppe was calculated as mean distance (in hundreds of kilometers) from cells designated as Steppe. The elevation (in kilometers) variable is the same as in the simulation. Finally, the approximate distribution of horse-based forms of warfare in each era was estimated from several sources (Figure S10)(10-22). In the first era, this was primarily chariot-based warfare, but later involved mounted cavalry. This variable can take one of four values (0, 1, 2, 3) depending on the number of eras a cell had horse-based warfare present. It is treated as continuous for the purposes of these analyses. Each predictor variable was entered alone and in combination with others to assess their relative importance and contribution to the overall model. Table SM5 shows the standardized SAR coefficients (i.e. after taking into account the effects of spatial autocorrelation).



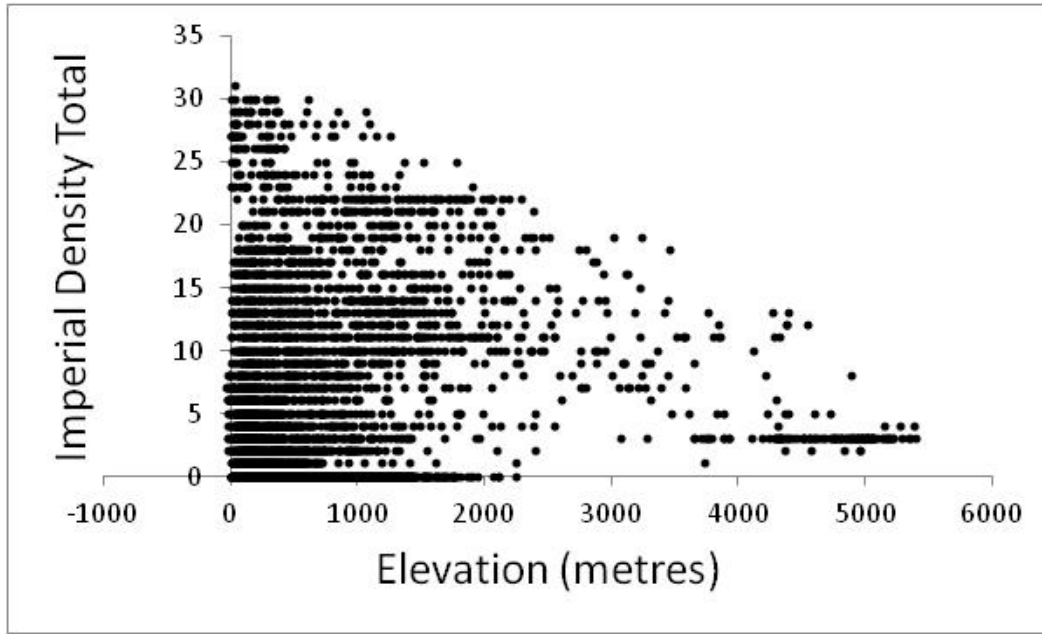
**Figure S10.** Estimated distribution of horse-based warfare across eras: All eras (dark blue), Era II & III (mid-blue), Era III only (light blue).

**Table SM5.** Standardized parameter estimates, AIC (Akaike Information Criterion adjusted for small sample size, AICc), and  $R^2$  values of predictor variables in different SAR models. ‘Agriculture’ = long-term presence of agriculture; ‘Steppe’ = distance from the Steppe; ‘Elevation’ = average elevation (in km), ‘Horse’ = horse based warfare (chariots for Era I, cavalry for Eras II and III). All parameter estimates are significant at  $P < 0.001$ .

Model	AIC	$R^2$	Agriculture	Steppe	Elevation	Horse
Full	16519.0	0.53	0.09	-0.28	-0.09	0.27
Only horse warfare	17031.6	0.43	–	–	–	0.38
Full without horse	17103.5	0.42	0.10	-0.47	-0.10	–
Steppe & agriculture	17184.7	0.40	0.09	-0.44	–	–
Steppe & elevation	17323.7	0.36	–	-0.48	-0.10	–
Only steppe	17365.2	0.35	–	-0.45	–	–
Agricult. & elevation	18346.0	0.06	0.12	–	-0.07	–
Only agriculture	18351.7	0.06	0.11	–	–	–
Only elevation	18518.9	<0.001	–	–	-0.07	–

The best-fitting model is one in which all predictor variables are present. The model explains around 53 percent of the variance in total imperial density over the time period we have considered here. Distance from the Steppe and the presence and duration of horse-based warfare are the two best predictors of total imperial density. This is in line with our theoretical model, which stresses the proximity to the Steppe and intense forms of warfare in selecting for large-scale forms of organization. The long-term presence of agriculture is a weaker predictor of imperial density (however, remember that the analysis considers only cells that did acquire agriculture by 1500 CE). This suggests that while agriculture is certainly a pre-condition for the evolution of large, complex societies variation in the timing of the introduction of agriculture itself may be less important in explaining why some areas have consistently been home to the largest-scale societies while others have not. Compare, for example, China and the Middle East, with New Guinea and Sub-Saharan Africa; all regions in which agriculture has been practiced for long periods but with very different histories with respect to the emergence of large-scale societies. Creation and retention of norms/institutions of large-scale organization is important – some regions into which agriculture expanded rapidly developed complex societies (e.g. East Europe), while others did not (e.g. southern Africa).

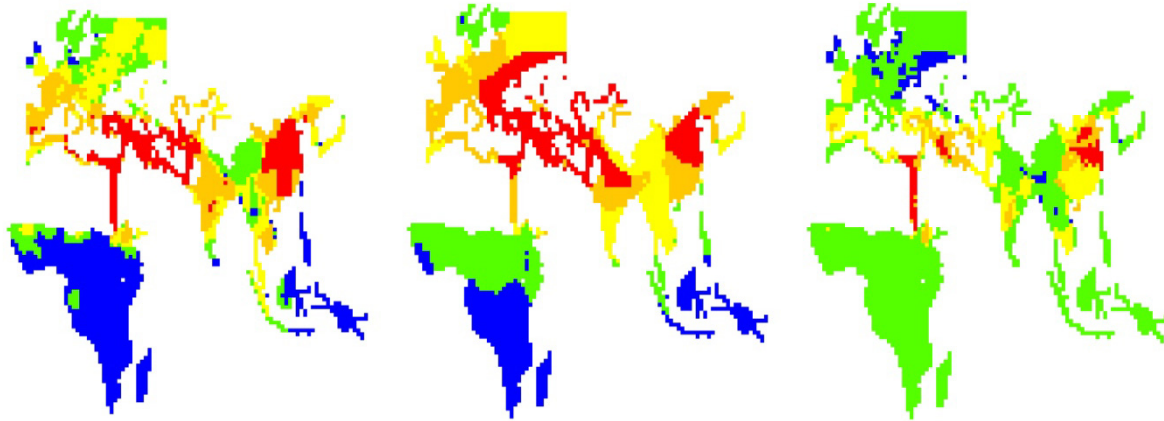
The weakest predictor was elevation, which, although a statistically significant predictor, does not contribute greatly to the amount of variation explained in these models. However, visual inspection of the data (Figure S11) indicate that elevation appears to be acting as a constraining factor rather than an active driver of imperial density. In other words, although complex societies tend not to form or spread to regions of high altitude and rugged topography, there are many flat, low-altitude regions where large-scale societies did not form.



**Figure S11.** The maximum value of imperial density decreases with increasing elevation. Many regions of lower elevation did not consistently develop large polities. This indicates that high elevation acts as a limiting factor on the creation of complex societies.

Although in these analyses our horse-based warfare variable is a slightly better predictor than distance from the steppe, both variables appear to explain similar parts of the variance and it should be stressed that our estimation of the distributions of these military technologies is only approximate. Future work will improve the temporal and spatial resolution of this variable and can even look at the development of particular aspects of military technology. This may allow a stronger test of the order in which warfare intensity and the development of large-scale organization develop. However, regardless of the precise times at which these technologies developed and spread, the broad outlines represented in our estimated distributions are expected to be reasonable in relative terms (i.e. chariots developing first in regions adjacent to the steppe, with cavalry spreading out later).

If we plot the estimated values based on the SAR coefficients from the best analysis (Figure S12) we can see that the SAR model does well at predicting which regions were more frequently home to large societies and in which region such societies did not form. It is important to point out that although the SAR model is predicting areas in which empires were more frequent relative to other areas, the maximum absolute values of these predicted scores (~13) do not reach the maximum observed values (i.e. 31). Plotting the residuals from the SAR analysis we can see that although the SAR model does well at predicting values for much of the area considered, it under-predicts the values for imperial density in the hotspots of empire formation (the middle east, Egypt, and China), while slightly over-predicting some regions such as eastern Europe, and Scotland and Northern Ireland.



A. Total Imperial Density

B. Predicted Density

C. Residual

**Figure S12.** Comparison of observed imperial density against SAR predicted values show the model does well at predicting regions of relatively high and relatively low imperial density. Observed and predicted category designations were based on portioning the data into quintiles. The five quintiles, from lowest to highest are blue, green, yellow, orange, and red. Predicted density categories are depicted in the same way. Residuals from the SAR analysis show most regions are well estimated (key blue: -10.2 to -5, green: -5 to 5, yellow: 5 to 10, orange: 10 to 15, red: 15 to 20.2, i.e green cells are those where predictions match observed values within 5 points). The model generally under-predicts the frequency with which cells were occupied in regions that were actually hotspots of empire formation.

In order to assess how important is the spatial autocorrelation component in explaining the fit between the simulated and historical data we also ran SAR analyses using the simulated data from the best parameter set as a predictor of the historical data. We ran analyses looking at 1) the total imperial density over the entire time span, and 2) imperial densities within each of three eras. The results of these analyses are summarized in table SM6. The results show that even factoring out the effect of spatial autocorrelation, the simulation still explains almost half the variance in our estimates of overall imperial density, compared to an estimate of 66% from OLS regression. Considering each era in turn also sees the  $R^2$  value drop between 15 and 24%. Taking spatial autocorrelation into account does not, thus, affect the qualitative pattern of results with the simulation being a better predictor of imperial density in era 2 than in eras 1 and 3. We continue to use the OLS  $R^2$  as our metric for the match between model predictions and data because spatial autocorrelations are not simply noise to be tuned out, but a result of processes explicitly built into the model (spatial diffusion of MilTech traits, spread of ultrasocial traits from a cell to a neighboring cell when it is conquered and undergoes ethnocide).

**Table SM6.** Comparison of  $R^2$  values between OLS regression and SAR analyses for the simulated data from the best parameter set as a predictor of imperial density for each era and overall.

Time Frame	OLS	SAR
Overall	0.66	0.47
Era 1	0.52	0.29
Era 2	0.67	0.52
Era 3	0.49	0.25

## IV. Supporting Discussion

### *IV.1 Limitations of the Approach*

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. Our decision to collect historical data only at 100-year time-slices means that the model ‘misses’ peaks of some substantial polities such as the Empire of Alexander the Great, or Attila’s Hunnic Empire. This could be seen as a limitation for traditional historical analyses because we have not included a few polities known to be historically influential. However, for the purposes of our analyses this is actually strength. Using a regular sampling strategy 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 only focused on the largest polities, i.e those that were approximately greater than 100,000 km<sup>2</sup>. This means that some complex societies, such as the Ancient Greek city states, are not included in our database. The focus on territorial extent is also a result of our attempt to be systematic and minimize bias, and this large threshold was chosen for practical considerations. Historical information about the world varies partly in the degree to which modern societies can invest in uncovering it. Our information about the history of western civilization, thus, is disproportionately good compared to some other parts of the world. Employing a relatively large cut-off minimizes the risk of “missing” polities with large populations in less well-documented regions and time-frames, because the larger the polity the more likely it is to have left some trace in the historical record. At a smaller threshold there are simply too many polities about which we have very little information, including their territories, and the effects of a bias in our access to the historical record is increased. Despite the complications involved in trying to estimate the historic distributions of complex societies, the broad, qualitative pattern identified in our dataset is likely to hold. Large societies first arose in Egypt, the Middle East, and Northern China, and then spread later to Europe, Central, South and Southeast Asia. Such societies were largely absent in sub-Saharan Africa (except for the Sahel region), and in other tropical regions, such as New Guinea. Finally, because we have focused on the largest polities in this model we have operated at quite a coarse grain of analysis. It would of course be possible to use smaller grid cells, however, this would be of limited value given the nature of these data and the goals of our present analysis. Adjusting the size of the grid cells may affect particular estimates of parameter values and overall model fit, there is no reason to suspect that it would affect the overall pattern of our model’s predictions, as long as model parameters are scaled appropriately as the resolution is increased. In other words, models without the effect of warfare intensity diffusing from the Steppe, and elevation would still do worse regardless of the cell dimensions.

A further limitation is the coarse grain at which we model the cultural traits, and the underlying ecology. We have deliberately kept our cultural traits quite abstract in order to facilitate model building; any simulation has to find a balance between attempting to be realistic, and being simple enough to understand the processes being modeled (23). Future work, will build on this simple model, introducing such extensions as explicit hierarchical organization, varying the strength of different traits, or having traits with more specific effects on group stability. Also, conceptually, cultural variation is often represented as a set of binary variables in cross-cultural analyses (24, 25). Complex variables, such as bureaucracy, can be ‘binarized’ by asking a series of yes/no questions: are bureaucrats full-time or part time? Is there an examination system? etc. This approach is especially useful in functional analyses, where cultural traits may



appear quite different, but actually perform similar underlying functions. Furthermore, agriculture is treated simply as being present or absent and its extent only varies at three points. However, some regions are more productive than others and, therefore, have a greater ability to support large populations and complex societies. Nevertheless, the relationship between agricultural productivity and social complexity is by no means straightforward, and agricultural productivity itself will vary as a function of climatic factors, the type of crop being grown, and the technology and techniques used in farming. Also we model desert cells as being unable to support complex societies; however, the imperial density maps indicate certain desert regions, particularly the Iranian plateau, actually having dense concentrations of macrostates. Although the coarse-grain modeling of the environment is suitable for our present purposes, in future work we will develop a more detailed picture of the resource base underpinning large-scale complex societies (producing finer-grained maps with smaller cells—50 x 50 km, and even 10 x 10 km), which will allow us to consider these and other complexities. It is important to note, as discussed above, that these errors are not biased towards providing support for our particular hypothesis. Indeed it is remarkable that our model is able to simulate data that match well the observed data in spite of these limitations.

We have chosen to focus on agrarian societies during a particular time frame and in a particular part of the world. We do not model the Americas, even though a number of large-scale societies, such as the Aztecs and Incas, developed there historically. However, Turchin has previously argued that similar processes, (i.e. interaction between groups on either side of an ecological frontier, and increasing intensity of warfare) may also explain the emergence of large-scale societies there (26). Recently, a group of anthropologists and archaeologists (reported extensively in a special issue of *Evolutionary Anthropology*) have proposed that the diffusion of bow-and-arrow technology had a major impact on the evolution of social complexity within North America (27). In future work we can assess whether using our model, but substituting archery in place of cavalry, may predict spatio-temporal patterns in the Americas. Furthermore, as the Old and New Worlds were almost completely isolated from one another until just before the end of the time frame we have considered in this study, examining the development of complex societies in the Americas would represent an interesting “natural experiment” in history (28). Our model performs very well in Afro-Eurasia for the period of 1500 BCE to 1500 CE, when horse-based warfare was the most important factor in elevating the intensity of competition between societies. The question arises, will a suitably updated version of the model do as well for the post-1500 CE period? It is clear that the model would have to focus on such new military technologies as gunpowder weapons and ocean-crossing ships (29, 30) and on economic competition (31). Plans are underway for developing such a model and testing it with the post-1500 data.

#### IV.2 *Broad Implications of our Research*

Our results potentially have implications for understanding the degree of inequality in wealth and material security in the modern world. Recent research indicates that present-day economic development and political stability have deep historical roots. Jared Diamond (6) argued that the initial endowments of continents in terms of domesticable plants and animals, and East-West vs. North-South orientation had determining impacts on subsequent political and economic development. Olsson and Hibbs (32) analyzed empirical evidence from a large cross-section of countries, and found that their results supported Diamond’s hypothesis. They concluded that geographic and initial biogeographic conditions exert decisive influence on transition to

sedentary agriculture, to complex social organization, and to modern industrial production. In other words, events that happened as far back in history as 10,000 years ago (domestication of plants and animals) shaped, and continue to affect the fates of modern nations. In a recent analysis, Comin et al. (33) assembled a dataset on technology adoption in 1000 BC, 0 AD, and 1500 AD. They found that technology in 1500 AD was strongly correlated with per capita income and technology adoption today. In turn, the situation in 1500 AD was strongly influenced by that in 0 AD, and 0 AD was correlated with 1000 BC. Bockstette et al. (34) broadened the scope of analysis to political variables and found that ‘state antiquity’ (an index of the depth of experience with state-level institutions) was significantly correlated with political stability, institutional quality, and the rate of economic growth between 1960 and 1995. The ability of populations to construct and maintain viable states is also strongly conditioned by history. For example, the efficiency of provincial governments in Italy is strongly correlated with the vibrancy of civic life in the province during the Renaissance (35). In fact, the roots of the North-South split in the ability to cooperate may go all the way to the times of the Late Roman Empire (36). The ability of different regions of Afghanistan to maintain local peace and order is similarly strongly conditioned on the previous history of state building in the region (37). Furthermore, ability to cooperate in the political and the economic spheres are probably interrelated (38).

It should not be surprising that political and economic development are closely correlated, and, in fact, may be just two different manifestations of the same deep structural process. Building viable states and vibrant economies requires huge numbers of people to cooperate on a very large scale (39). In this paper we have followed the work of a number of theorists who have argued that the human capacity for cooperation in huge groups of genetically unrelated individuals, is due to the evolution of ultrasocial norms and institutions (40-42). Many social scientists also stress the importance of institutions in explaining variation in modern-day development. For example, Acemoglu et al. (43) pointed out that a number of areas that were highly developed prior to 1500 AD experienced severe reversals as a result of European colonization. They argue that in the unhealthy tropical regions, where Europeans could not settle, they set up highly extractive institutions, which destroyed the future prospects for economic growth and political development. They claim that “once the effect of institutions is controlled for, countries in Africa or those closer to the equator do not have lower incomes.” In a similar vein, the analysis by Nunn and Puga (44) connected poor institutional development within Africa to regions that historically were under the greatest pressure from slaver raids. Yet another direction has been explored by Enrico Spolaore and co-workers, who have focused on the ancestral composition of current populations (45). Institutional-based explanations are sometimes contrasted with other theories that stress exogenous factors (38). Some authors, such as Jared Diamond and Jeffrey Sachs, argue for a direct effect of geography on economic growth, focusing on such mechanisms as disease burdens. For example, there is a striking correlation between malaria and poverty (46).

These examples demonstrate that although there are strong empirical patterns linking history and geography to the current distribution of world wealth and political stability, there is as yet no agreement on the processes underlying these patterns. We argue that the dichotomy between institutional explanations on the one hand and geographic or ecological on the other is a false one. Our model encapsulates one set of mechanisms that may explain how geographic and historical influences interact in enabling the evolution and persistence of ultrasocial institutions. In our model the formation of large groups is a product of historical factors (e.g. the evolution of cultural institutions), and geographic factors (e.g. terrain), while some factors have both

historical and geographic elements. 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 horse for domestication). In our model the key mechanism is the elimination of groups and societies that fail to acquire, or lose ultrasocial institutions via a process of cultural multilevel selection (CMLS). Because the intensity of between-group competition varies in space and time, we were able to test the model's predictions empirically.

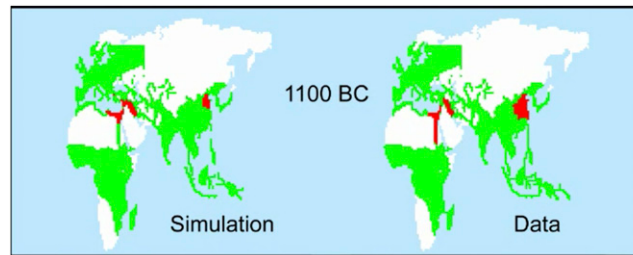
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# Supporting Information

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**Movie S1.** Comparison between the distributions of large-scale polities in the historical data (right-hand side) and the data generated by the simulation model (left-hand side) for each time slice over the period 1,500 BCE to 1,500 CE.

[Movie S1](#)

## Other Supporting Information Files

[SI Appendix \(PDF\)](#)