Transition to farming more likely for small, conservative groups with property rights, but increased productivity is not essential

Elizabeth M. Gallagher,[a,b,1] Stephen J. Shennan,[c] and Mark G. Thomas[a]

[a]Research Department of Genetics, Evolution, & Environment, University College London, London, WC1E 6BT, United Kingdom;
[b]Centre for Mathematics, Physics, and Engineering in the Life Sciences and Experimental Biology, University College London, London, WC1E 6BT, United Kingdom;
[c]Institute of Archaeology, University College London, London, WC1H 0PY, United Kingdom
[1]To whom correspondence should be addressed. Email: e.gallagher.12@ucl.ac.uk.
Edited by Bruce P. Winterhalder, University of California, Davis, CA, and accepted by the Editorial Board September 19, 2015 (received for review June 21, 2015)

SIGNIFICANCE

The Neolithic revolution was one of the most influential events in human history, but why and how it occurred are still not fully understood. To try to infer what may have happened, mathematical models have been developed. We describe and implement a method of parameter space exploration when ideal outcomes of a model are known. This method is applied to a published agent-based model for the Neolithic transition, revealing previously unidentified parameter interactions, sensitivities, and complexities. Our results highlight the importance of group structuring, group size, conservatism, and farming-friendly property rights, for the switch to farming around 12,000 years ago. We also find that, although advantageous, it is not essential that farming productivity is greater than foraging productivity.

Keywords: Neolithic revolution, simulation, agent-based modeling, fitting to idealized outcomes, property rights

ABSTRACT

Theories for the origins of agriculture are still debated, with a range of different explanations offered. Computational models can be used to test these theories and explore new hypotheses; Bowles and Choi [Bowles S, Choi J-K (2013) *Proc Natl Acad Sci USA* 110(22):8830–8835] have developed one such model. Their model shows the coevolution of farming and farming-friendly property rights, and by including climate variability, replicates the timings for the emergence of these events seen in the archaeological record. Because the processes modeled occurred a long time ago, it can be difficult to justify exact parameter values; hence, we propose a fitting to idealized outcomes (FIO) method to explore the model's parameter space in more detail. We have replicated the model of Bowles and Choi, and used the FIO method to identify complexities and interactions of the model previously unidentified. Our results indicate that the key parameters for the emergence of farming are group structuring, group size, conservatism, and farming-friendly property rights (lending further support to Bowles and Choi's original proposal). We also find that although advantageous, it is not essential that farming productivity be greater than foraging productivity for farming to emerge. In addition, we highlight how model behaviors can be missed when gauging parameter sensitivity via a fix-all-but-one variation approach.

After around 190,000 y of anatomically modern humans living as hunter-gatherers, societies began to make a transition to agricultural subsistence systems. These transitions are thought to have occurred independently in several regions of the world between 11,500 and 3,500 y before present (yBP) (1), and farming has spread to most

of the world from these centers. This transition had major impacts on human demography, evolution, diet, health, culture, technology, and social inequality (2–5). It is generally agreed that there are at least three separate regions around the world where agriculture originated independently: the Fertile Crescent, Mesoamerica, and China (1, 2, 5). There is also growing evidence for additional independent origins of domestication, which include the eastern United States, the Andes, the Central and South America tropics, New Guinea, West Africa, and southern and northern India (5).

A range of different explanations for the development of agriculture have been proposed, including some based on affluence and social competition [e.g., via feasting (6)] and others based on stress [e.g., because of population pressure (7) or climate changes (8)]; some propose revolution (e.g., 9), and some suggest changes were made consciously (e.g., 10), whereas others argue changes were made unconsciously (e.g., 11) (1). Whereas the long-term advantages of farming are clear in that it is a strategy that has generally led to increased carrying capacities and greater reproductive successes when adopted (12), the short-term fitness payoffs are less obvious, and it is increasingly recognized that key changes in social institutions would have been necessary (13).

COMPUTATIONAL APPROACHES   Go to:

Investigating the reasons behind the transition to agriculture is problematic because modern ethnographic data may not be informative on ancient population dynamics, and the material culture record is sparse and only weakly informative on social aspects of the transition. Furthermore, the appearance of domestication traits in various species is likely to postdate their initial cultivation or management, sometimes by some considerable margin (14). In this context, computational models can be helpful in exploring the ecological and social conditions necessary for the transition to agriculture. There are many examples of such models [e.g., 13, 15–22; also the modeling review by Baker et al. (23) and discussion of modeling approaches by Gerbault et al. (24)], which, together, have explored most of the major hypotheses for the origins of agriculture (most notably, climate and population pressure).

BOWLES AND CHOI MODEL   Go to:

It has been argued that during the transition to agriculture, the institution of private property emerged (25–27). This idea led Bowles and Choi (13) to hypothesize that the advent of farming was impossible without farming-friendly property rights, and vice versa. Furthermore, they posit that farming was not suddenly invented and then adopted because it was a "better way to make a living" (13) but, instead, that it was only due to particular rare (and perhaps coincidental) environmental and social conditions that it became established. To study these hypotheses, an agent-based model was developed (henceforth referred to as the Bowles and Choi model), calibrated with a proxy of climate volatility [the $^{18}O/^{16}O$ ratio in the North Greenland Ice Core Project (NGRIP) ice core (28–31)]. Their simulations show that farming and farming-friendly property rights can coevolve with approximately the same timings and magnitude as indicated in the archaeological record.

The Bowles and Choi model (13) is based on 600 agents (the hypothesized size of "a late Pleistocene ethnolinguistic unit"), separated into groups of 20 (the size of "forager bands or small villages"). Agents have two types of strategies: They can be farmers or foragers (their "technology strategy"), and they can have a "behavioral" strategy, whereby they can be a sharer, a bourgeois, or a civic (explained later). The model can be split into five sections: within-group interactions, between-group interactions, cultural updating, behavioral experimentation, and migration. All simulations start with a population of civic foragers, representing what may be expected in the late Pleistocene on the basis of generalizations from hunter-gatherer ethnographies (32).

First, agents obtain their payoffs by foraging or farming. The productivity of foraging, V_h, is normalized to 1, and the productivity of farming is $V_a = (r - \theta) z - z$, where r is the productivity of the farmer's investment, z is the amount of farming investment, and θ is the disadvantage of farming due to temperature volatility [θ is found by transforming the original NGRIP ice core data to find a value for each 20-y period; details can be found in Bowles and Choi's supporting information (13)]. Hence, the value for the productivity of farming changes every 20 y, and iterations of the model are now pegged to specific years. Next, two agents from the same group are randomly paired, and games are played over the distribution of each of the agents' products. The outcomes of these games can increase or decrease the agents' payoffs based on which strategies they both have (*SI Appendix*, section S1). Key components of this model are the farming-friendly property rights of the bourgeois agents and the "sharing-enforcer" role played by the civics. A bourgeois agent will never share its own product, it will never contend for a farmed product (the contestability of farming, μ_a, is 0), and it will always try to steal a foraged product (the

contestability of foraging, μ_h, is 1). This behavior is not tolerated by civics, which try to punish the bourgeois individual. Hence, there will be contests between civic foragers and bourgeois agents. If the civic wins, which happens with a probability (f) that increases with the number of civics in the group, the product is shared equally between all of the civics in the group, and the bourgeois pays the conflict cost, C. Alternatively, the conflict cost is divided between all of the civics in the group. Thus, these within-group conflicts will not occur if the population consists of either entirely civic or sharer foragers (i.e., the Pleistocene state) or entirely bourgeois farmers (i.e., the Holocene state). Sharers never participate in contests, either sharing or conceding their product depending on whom they interact with.

With a probability κ, all of the groups are randomly paired and between group contests can occur (where contests are less likely between equally matched groups, and the group with the higher average payoff is more likely to win). Each of the agents in the winning group then gains τ payoff units each, and agents from the losing team lose τ payoff units each.

Next, agents are assigned a cultural model for both strategies. Cultural models are generally chosen from within the same group, with the exception of the loser of a between-group interaction, where cultural models are chosen from the winning group. Cultural models are more likely to be from the predominant type of strategy, with the probability that a sharer, bourgeois, or civic is chosen as the cultural model as, respectively, α^η/y, β^η/y, or $(1-\alpha-\beta)^\eta/y$, where $y = \alpha^\eta + \beta^\eta + (1-\alpha-\beta)^\eta$, α and β are the proportions of sharers and bourgeois within the group, and η is a measure of conformist biased cultural transmission. An agent will copy their cultural model's strategy if it has a higher payoff.

The last stages in the model are behavioral experimentation, where agents will randomly change their strategies with probability ε, and migration, where agents migrate from their group with probability m and are randomly assigned to another group.

Bowles and Choi ([13](#)) ran 1,000 simulations of their model over 2,075 iterations (41,500 y) and recorded the percentage of simulations at each iteration that had more than 50% bourgeois farmers. Their results ([Fig. 1](#)) show a small increase in the number of bourgeois farmers around 15,000–13,000 yBP; this small increase is noted to coincide with short-lived experiments in sedentism and storage seen in the Natufian culture. After around 11,000 yBP, there is a steady increase in the number of majority bourgeois farmer simulations, fitting with evidence that independent origins occurred after this point in all of the well-studied regions. For any given year, there are always less than 31 of the 1,000 simulations with a bourgeois farmer majority.
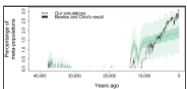

[Fig. 1.](#)

Range (light green), interquartile range (middle green), and median (dark green) of the percentage of metapopulations (1,000 simulations) with a majority of bourgeois farmers at each time point when running our interpretation of the model 1,000 times. **...**

FITTING TO IDEALIZED OUTCOMES

Choosing default or initial parameter values in computational models can be difficult, because well-evidenced values are not always available. Furthermore, testing a model's sensitivity to a known range of parameter values can be complicated when there are many parameters. Usually parameters are varied one-by-one while keeping the others at their default values; however, this approach will overlook most interactions between parameters, and poses problems in choosing realistic default values.

Bowles and Choi ([13](#)) test the robustness of their model by varying parameters one-by-one, and show that varying parameters through plausible values gives the same outcome as the result with the default parameters, although with changeable magnitudes (*[SI Appendix, section S3](#)*). We expanded on this analysis by running the model 1.2×10^7 times with randomly chosen (within defined limits) combinations of parameters ([Table 1](#)), selecting the simulations closest to idealized outcomes (the "top" simulations), and then exploring the patterns and interactions of the parameter values in these top simulations. This fitting to idealized outcomes (FIO) method examines parameter sensitivity in the model and can also be used to predict scenarios in which farming could develop, which were otherwise unconsidered in the original work. The FIO approach is similar in principle to approximate Bayesian computation ([33](#)), except that simulated data are fitted to an idealized outcome instead of empirical data; in this

case, the idealized outcome is the maximum proportion of farmers 9,000 yBP, when farming is generally believed to have become well-established in southwestern Asia ([34]).

[Table 1.](#)

Model parameters, their default value used in the Bowles and Choi model, and the range of values sampled from in the FIO analysis if applicable

RESULTS

Of the 1.2×10^7 simulations run, only ~13% have a majority (>300) of farmers at 9,000 yBP, and only ~1% of simulations have over 500 farmers (*SI Appendix*, Fig. S3). From Fig. 2, we can see the relative frequencies of parameter values when considering the top 1%, 0.5%, and 0.1% of simulations. A simulation's placement in the top 1% of simulations is very sensitive to g, ε, V_h, μ_a, and V_a; moderately sensitive to C and η; and relatively insensitive to m, μ_h, τ, and κ (statistics are provided in *SI Appendix*, Table S3). Correlation coefficients between the number of farmers and parameter values are shown in Table 2. These trends can be clearly seen for the top 1% of simulations in *SI Appendix*, Fig. S4, and for all of the simulations in *SI Appendix*, Fig. S5.
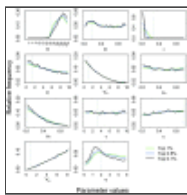

[Fig. 2.](#)

Relative frequency plots of parameter values for different top slices of the 1.2×10^7 simulations (top 1% in green, top 0.5% in blue, and top 0.1% in black). The vertical dashed lines show the default values chosen by Bowles and Choi ([13]). For **...**

[Table 2.](#)

Spearman's rank correlation coefficients, ρ, between parameter values and the number of farmers in different top slices of the 1.2×10^7 simulations

Parameter interactions, as indicated by correlations between pairs of parameters in the top 1%, 0.5%, and 0.1% of simulations, are shown in Fig. 3 (coefficients are given in *SI Appendix*, Table S4). The largest of these correlations were between g and ε ($\rho = -0.402$), V_h and V_a ($\rho = 0.376$), and ε and η ($\rho = 0.359$). The relationship between behavioral experimentation (ε) and the number farmers for low, medium, and high numbers of groups (g) can be seen in Fig. 4, and for all groups in *SI Appendix*, Fig. S6. Here, we see that increasing the amount of behavioral experimentation (ε) can increase the amount of farming (Fig. 4), but the highest numbers of farmers are mostly found in simulations where g is large and behavioral experimentation is low (Fig. 4, *Right*). For the productivities of foraging and farming (V_h and V_a, respectively), we find that in the top 1% of simulations, farming is almost always more productive than foraging (i.e., $V_a/V_h \geq 1$, for 98.1% of these simulations). However, when we look at all simulations (Fig. 5), we find that there are some (3.66%) with a majority (>300) of farmers when $V_h > V_a$ holds. The relationship between behavioral experimentation (ε) and the level of conformism (η) in the top 1% of simulations can be seen in Fig. 3. It is only for smaller values of η (< 2) that we see a relationship between lowering ε and there being a greater number of farmers. We see little change in the effect of ε while increasing η greater than around 2.
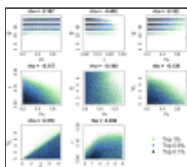

[Fig. 3.](#)

Eight significant largely ($|\rho| > 0.1$) correlated pairs of parameters in the top 1% of the 1.2×10^7 simulations. These plots are broken down into all of the top 1% simulations (green, blue and black points), top 0.5% (blue and **...**
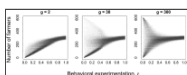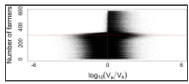

[Fig. 4.](#)

Relationship between behavioral experimentation (ε) and the number of farmers for simulations with different numbers of groups (g): $g = 2$ (*Left*), g = 30 (*Middle*), and g = 300 (*Right*) (each point represents one simulation). Thus, when groups are **...**

[Fig. 5.](#)

Ratio of farming productivity to foraging productivity (V_a/V_h) and the numbe... 1.2×10^7 simulations; a $\log_{10}(V_a/V_h)$ scale is used. The vertical red line sho... is 1 (i.e., $V_a = V_h$), and the horizontal red line **...**

DISCUSSION

Our analysis has highlighted that the parameters g, ε, V_h, μ_a, and V_a (or z) are the most influential parameters on the number of farmers at 9,000 yBP in the model. Therefore, we suggest that group structuring, behavioral experimentation, property rights, and the ratio of farming productivity to foraging are most important for the emergence of farming using this model.

Structuring. Our work has highlighted the relationship between the number of groups (g) and the amount of behavioral experimentation (ε) (Fig. 4). By increasing ε, we see an increase in the number of farmers. However, this increase converges to around 50% farmers, because when ε is large, agents are changing regularly between both strategies and there is little structuring in the group. It is only when the number of groups is large (i.e., the groups are small) that we start to see more simulations that have a majority of farmers. Because the simulations all started with a civic forager population, it could be that a single farmer in a large group would be more at a disadvantage than it would in a smaller group, and hence farming would be less likely to emerge as a majority. In fact, it is increasingly unlikely that a bourgeois will win a civic-bourgeois contest in a civic majority group when groups are large (*SI Appendix*, section S8). When groups are smaller, we also see that there are more majority farmer simulations as the behavioral experimentation decreases; possibly because high values for ε disrupt any structuring, resulting in property rights and farming failing to coevolve. Hence, we predict that farming should emerge when there is low behavioral experimentation and groups are as small as possible (groups smaller than around four or six members are ethnographically improbable anyway). Interestingly, this prediction is consistent with some models of the emergence of prosocial behavior, whereby cooperation (of which farming property rights are an example) is unlikely to emerge in large groups (35–37).

Conservatism. Another finding of this work is that to generate large numbers of farmers or foragers, behavioral experimentation (ε) should be low (Fig. 2). Because the model starts with all foragers, to generate farming, ε must not equal 0. However, as behavioral experimentation approaches 1, there will be equal numbers of foragers and farmers, because people will be constantly switching from one to the other as explained above. Hence, we predict that conservatism (which we define as a low rate of switching between strategies) helps the emergence of farming, and so long as farming is introduced into the population, it will be selected for.

Property Rights. Our analysis lends further support to the conclusion by Bowles and Choi (13) that farming and farming-friendly property rights can coevolve. One illustration of this support is that although our simulations allowed there to be no property rights (which is when farming property is always contested, $\mu_a = 1$), we still see a greater proportion of farmers as the contestability of a farmed product (μ_a) approaches 0 (Fig. 2). Conversely, we also find that varying degrees of property rights for foraged products, μ_h, has little influence on the number of foragers (as seen by the absence of any trend in the μ_h panels of Fig. 2 and *SI Appendix*, Figs. S4 and S5, and by the low correlation coefficients in Table 2). Furthermore, the relationship between μ_a and the number of farmers appears similar to one of exponential decay as the size of the top slice is decreased (Fig. 2). This trend would be expected if farming-friendly property rights were a main cause of farming in the model.

Ratio of the Productivity of Farming to Foraging. We have also seen that the productivity-of-farming to productivity-of-foraging ratio (V_a/V_h) has an important effect on farming, where $V_a > V_h$ almost always holds in the top 1% of simulations. However, there are some simulations with a majority of farmers where $V_a < V_h$ (Fig. 5). Thus, there are cases where farming emerges despite the productivity of foraging being greater than the productivity of farming. This observation lends some support to the result of Bowles' study (38), where it was found that the productivity of farming did not need to be greater than the productivity of foraging for early farmers.

Cost of Conflict and the Level of Conformity, C and η. The proportion of farmers at 9,000 yBP was moderately sensitive to parameters C and η, the cost of conflict and the level of conformity, respectively. The frequency decrease as the cost of conflict is increased (Fig. 2) may be because this change has the most impact on bourgeois agents, as civic foragers share the cost. Because we have seen that farming is increased by farming-friendly property rights, fewer bourgeois agents would mean fewer farmer agents. Thus, costly conflicts result in less farming in this model.

For η, the level of conformity, the highest frequency value in the top simulations approaches around $\eta = 1$ as the top slice gets smaller (Fig. 2). This result may be because as η increases, if a strategy's frequency is below 0.5 in the group, it is increasingly unlikely that this strategy will be a cultural model for another agent (figure S3 of ref. 1); thus, this strategy may have little chance of propagating in the population. Hence, for a farming strategy (which starts from a frequency of 0) to become the main strategy in a population, η cannot be too large. On the other hand, at $\eta = 0$ (no conformity), the probability that a farmer or a forager agent will be selected as a cultural model is always 0.5 independent of frequencies in the group; therefore, we see most simulations leading to a near 1:1 farmer/forager ratio (SI Appendix, Fig. S5). Thus, for farming to do well in this model, there should be low (but nonzero) levels of conformity.

Insensitive Parameters. There were a number of parameters whose values were relatively unimportant for the emergence of farming in the model. These parameters were the migration rate (m), the contestability of a foraged product (μ_h; discussed earlier), the resource transfer amount (τ), and the probability of a between-group conflict (κ). Because varying κ and τ will affect agents' payoffs and the spread of farming or foraging equally, it might be expected that these parameters would not make a difference to the amount of farming. Thus, the likelihood and intensity (in terms of potential payoff losses and gains) of between-group conflicts are not driving forces in the emergence of farming in this model. If there was any intergroup violence associated with the Neolithic transition [although there is little evidence for it (39)], our analysis suggests it was caused by the transition, rather than causal of the transition.

The probability of migration between groups also makes little difference to the emergence of farming. Perhaps in this model, intergroup cultural updating drives the mixing of different strategies in the population, and so migration among well-mixed groups will not introduce new strategies into groups.

Assumptions and Caveats. As with all models, there are many assumptions and simplifications in the Bowles and Choi model (13). For example, would cultural updating be likely to occur for every agent at each iteration, would an individual's technology be as binary as "farmer" or "forager," and is it likely that foraging and farming productivity are independent of one another?

Whereas the Bowles and Choi model (13) and the analyses presented here are primarily concerned with the initial establishment of farming groups, other factors are likely to have influenced farming's growth, sustainability, geographical spread, and archaeological visibility. These factors include the availability of suitable plant and animal species for domestication, other local climate and ecological factors, and technological innovations, all of which are likely to affect the relative productivity of farming (V_a/V_h). In addition, it is likely that farming activity itself changes V_a/V_h, to varying extents in different regions, as a niche construction process (40).

An issue with our approach is making sure that enough simulations were collected, because insufficient simulations can result in poor assessment of model behavior. However, because the relative frequency plots in Fig. 2 do not change greatly with more narrow top slices, we are confident that running more simulations would have only smoothed these plots, rather than supporting different interpretations. Because this approach does not fit to empirical data, there could be another issue in finding what the "idealized outcome" should be. If there are multiple possibilities, as many as possible should be tested. In the case of this work, we found that using various other possible idealized outcomes (number of bourgeois farmers at 9,000 yBP, number of farmers at 0 yBP, and minimum and average number of farmers between 0 and 9,000 yBP) made very little difference to our overall results (SI Appendix, section S4). Furthermore, it is important to pick parameters from a sensible range of values. If the range covers unrealistic values, there will be unnecessary simulations; on the other hand, if the range does not cover all of the realistic values, there could be unseen trends. We have erred on the side of caution; most of our parameter ranges cover all plausible values (parameter ranges are justified in *Methods* and *SI Appendix*, section S7).

CONCLUSION

Here, we have replicated the results of the Bowles and Choi model (13) and implemented an FIO method to explore the parameter space and parameter interactions of this model. To our knowledge, this approach has not been used in archaeological modeling. We have also been able to hypothesize that a number of elements are key for the emergence of farming. These elements are as follows: a population structured into groups, small (but not too small) group sizes, a very low amount of behavioral experimentation, and the presence of farming-friendly property rights. We also found that although it is beneficial for farming when its productivity is greater than the productivity of foraging, it is not essential for its emergence; this result is consistent with previous findings (38). Additionally,

our results indicate that costly conflicts within the groups, and high levels of conformity when groups are culturally updating, result in less farming. Furthermore, we find that migration rate and the likelihood and intensity of between-group conflicts are unimportant for the emergence of farming in this model.

To an extent, our analyses contradict the robustness checks reported by Bowles and Choi ([13]) and reveal parameter complexities and interactions previously unrecognized. They have also allowed us to examine the effects of simultaneously varying parameters, which was not possible using the fix-all-but-one parameter approach. In comparison to Bowles and Choi's robustness checks (summarized in *SI Appendix*, section S3), the small range of variations in m led to an increase in farming using 1,000 simulations in Bowles and Choi's study ([13]), but we saw no overall effect when looking at the full range of m in over 10^3 times as many simulations. Similarly, when Bowles and Choi ([13]) increased the contestability of a foraged product (μ_h), the resource transfer amount (τ), and the probability of a between-group conflict (κ), they found a decrease in the amount of farming, whereas we found no significant differences. Furthermore, they found an increase in the amount of farming when increasing either the cost of conflict (C) or behavioral experimentation (ε), whereas we found a decrease in both cases. However, for an increase in the contestability of a farmed product (μ_a), we both predict that there will be a decrease in the amount of farming.

The findings from this analysis highlight key conditions for the origins of agriculture, which should be investigated in more detail in future studies (e.g., asking whether groups were small during the transition to agriculture). Our work highlights the problems of the fix-all-but-one parameter approach, and we hope it serves as an example of this type of parameter analysis in the field of computational modeling in archaeology as a means of exploring past processes.

METHODS

Replication. We first attempted to translate the published description of the Bowles and Choi model ([13]) to replicate their result. Our simulation code was written in C++ and is available on request. Several small errors were identified and corrected after discussion with Bowles and Choi (outlined in *SI Appendix*, section S2). Following these clarifications and using some of their code for the within-group interactions, we were essentially able to replicate their published results using the default parameter values.

To look at the variability in our results, we ran the model 10^6 times with the default parameters (given in Table 1) and then separated these simulations into 1,000 sets of 1,000 simulations. The range of the number of majority bourgeois farmer simulations at each year for all of these 1,000 simulation sets can be seen in Fig. 1, along with the published results of Bowles and Choi (which mostly fall into our range). We observed a similar trend to theirs, where the presence or absence of a majority of bourgeois farmers occurs at the same times, and a steady increase in bourgeois farmers also occurs from around 11,000 yBP to the present day. However, because there is no analysis of the variability between different runs of the model in the study by Bowles and Choi ([13]), it is not possible to determine whether our results fall into the range of their results.

Parameter Randomization and Ranking Simulations. We varied the following parameters from the Bowles and Choi model ([13]): g, V_h, z, μ_h, μ_a, C, κ, τ, η, ε, and m. Because the productivity of farming, V_a, is a function of r and z, we elected to vary only z. We kept the overall number of agents in the population at 600, the hypothesized size for an ethnolinguistic group in the late Pleistocene in the study by Bowles and Choi ([13]). There are 12 possible values for the number of groups, g, since g needs to be even, divide 600, and result in even-sized groups. The parameters that concern the addition or subtraction from payoffs (C, V_h, and τ) were given a range from 0 to 10 (justified in *SI Appendix*, section S7). We made the assumption that the maximum value for V_h is the same as for V_a, because there will be an upper limit to how much a person can benefit from food production. The productivity of farming will be at its maximum when the disadvantage of farming due to temperature volatility (θ) is minimized. Hence, rearranging the equation for V_a, we have $\max(z) = \max(V_a)/(r - \theta_{min} - 1) = 10/(1.5 + 0.0206 - 1) = 19.21$. The function that defines the probability of a trait being selected for a cultural model converges when η is increased (figure S3 of ref. [13]); hence, we only varied η between 0 (no conformity) and 5. The other parameters are probabilities, which we varied through the whole range from 0 to 1. The parameters, their default values, and their range of values varied are shown in Table 1.

Next, we ran simulations with parameter sets that were randomly chosen from the ranges discussed above. These simulations were then ranked on how close they are to an idealized outcome. Archaeological evidence indicates

that farming in the Near East had become established by the Late/Final Pre-Pottery Neolithic (9,500 to 8,800 yBP) (e.g., ref. 34), hence we ranked our simulations based on the number of farmers they have at 9,000 yBP, where the highest would be classified as the idealized outcome. This number stays roughly the same from 9000 to 0 yBP (*SI Appendix,* section S4); thus, our results can be applied other origins of farming in different regions of the world [because the Near East was the earliest (1)]. Note that we considered the number of farmers rather than bourgeois farmers in this analysis, although this difference has little impact on the results (*SI Appendix,* section S4). After running these simulations, the next step was to identify trends in the parameter values of the top simulations and correlations between closeness-of-fit rank order and parameter value.

SUPPLEMENTARY MATERIAL   Go to:

Supplementary File

Click here to view. (15M, pdf)

ACKNOWLEDGMENTS   Go to:

FOOTNOTES   Go to:

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. B.P.W. is a guest editor invited by the Editorial Board.

This article contains supporting information online at
www.pnas.org/lookup/suppl/doi:10.1073/pnas.1511870112/-/DCSupplemental.

REFERENCES   Go to:

1. Bellwood P. First Farmers: The Origins of Agricultural Societies. Blackwell; Oxford: 2005.

2. Diamond J. Evolution, consequences and future of plant and animal domestication. Nature. 2002;418(6898):700–707. [PubMed]

3. Starling AP, Stock JT. Dental indicators of health and stress in early Egyptian and Nubian agriculturalists: A difficult transition and gradual recovery. Am J Phys Anthropol. 2007;134(4):520–528. [PubMed]

4. Lambert PM. Health versus fitness: Competing themes in the origins and spread of agriculture? Curr Anthropol. 2009;50(5):603–608. [PubMed]

5. Fuller DQ. An emerging paradigm shift in the origins of agriculture. General Anthropology. 2010;17(2):1–12.

6. Hayden B. Nimrods, piscators, pluckers, and planters: the emergence of food production. J Anthropol Archaeol. 1990;9(1):31–69.

7. Cohen MN. Food Crisis in Prehistory: Overpopulation and the Origins of agriculture. Yale Univ Press; New Haven, CT: 1977.

8. Bar-Yosef O. The Natufian culture in the Levant, threshold to the origins of agriculture. Evolutionary Anthropology Issues News and Reviews. 1998;6(5):159–177.

9. Cauvin J. The Birth of the Gods and the Origins of Agriculture. Cambridge Univ Press; Cambridge: 2000.

10. Braidwood RJ. The agricultural revolution. Sci Am. 1960;203:131–148. [PubMed]

11. Rindos D. The Origins of Agriculture: An Evolutionary Perspective. Academic; New York: 1984.

12. Bocquet-Appel J-P. When the world's population took off: The springboard of the Neolithic Demographic Transition. Science. 2011;333(6042):560–561. [PubMed]

13. Bowles S, Choi J-K. Coevolution of farming and private property during the early Holocene. Proc Natl Acad Sci USA. 2013;110(22):8830–8835. [PMC free article] [PubMed]

14. Zeder MA. Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact. Proc Natl Acad Sci USA. 2008;105(33):11597–11604. [PMC free article] [PubMed]

15. Reynolds RG. An adaptive computer model for the evolution of plant collecting and early agriculture in the Eastern Valley of Oaxaca. In: Flannery KV, editor. Guila Naquitz: Archaic Foraging Early Agriculture in Oaxaca Mexico. Academic; Orlando, FL: 1986. pp. 439–507.

16. Locay L. From hunting and gathering to agriculture. Econ Dev Cult Change. 1989;37:737–756.

17. Winterhalder B, Goland C. On population, foraging efficiency, and plant domestication. Curr Anthropol. 1993;34(5):710–715.

18. Richerson PJ, Boyd R, Bettinger RL. Was agriculture impossible during the Pleistocene but mandatory during the Holocene? A climate change hypothesis. Am Antiq. 2001;66(3):387–411.

19. Wirtz KW, Lemmen C. A global dynamic model for the Neolithic transition. Clim Change. 2003;59(3):333–367.

20. Marceau N, Myers G. On the Early Holocene: Foraging to Early Agriculture. Econ J. 2006;116(513):751–772.

21. Dow GK, Reed CG, Olewiler N. Climate reversals and the transition to agriculture. J Econ Growth (Boston) 2009;14(1):27–53.

22. Dow GK, Reed CG. Stagnation and innovation before agriculture. J Econ Behav Organ. 2011;77(3):339–350.

23. Baker MJ. A structural model of the transition to agriculture. J Econ Growth (Boston) 2008;13(4):257–292.

24. Gerbault P, et al. Storytelling and story testing in domestication. Proc Natl Acad Sci USA. 2014;111(17):6159–6164. [PMC free article] [PubMed]

25. North DC, Thomas RP. The first economic revolution. Econ Hist Rev. 1977;30(2):229–241.

26. Earle T. Archaeology, property, and prehistory. Annu Rev Anthropol. 2000;29:39–60.

27. Bogaard A, et al. Private pantries and celebrated surplus: Storing and sharing food at Neolithic Çatalhöyük, Central Anatolia. Antiquity. 2009;83(321):649–668.

28. Andersen KK, et al. The Greenland ice core chronology 2005, 15–42 ka. Part 1: Constructing the time scale. Quat Sci Rev. 2006;25(23):3246–3257.

29. Svensson A, et al. The Greenland ice core chronology 2005, 15–42 ka. Part 2: Comparison to other records. Quat Sci Rev. 2006;25(23):3258–3267.

30. Rasmussen SO, et al. A new Greenland ice core chronology for the last glacial termination. J Geophys Res Atmos. 2006;111(D6):1–16.

31. Vinther BM, et al. A synchronized dating of three Greenland ice cores throughout the Holocene. J Geophys Res Atmos. 2006;111(D13):1–11.

32. Kaplan H, Gurven M, Hill K, Hurtado AM. The natural history of human food sharing and cooperation: a review and a new multi-individual approach to the negotiation of norms. In: Gintis H, editor. Moral Sentiments and Material Interests: The Foundations of Cooperation in Economic Life. MIT Press; Cambridge, MA: 2005. pp. 75–113.

33. Beaumont MA. Approximate Bayesian computation in evolution and ecology. Annu Rev Ecol Evol Syst. 2010;41:379–406.

34. Conolly J, et al. Meta-analysis of zooarchaeological data from SW Asia and SE Europe provides insight into the origins and spread of animal husbandry. J Archaeol Sci. 2011;38(3):538–545.

35. Nosenzo D, Quercia S, Sefton M. Cooperation in small groups: The effect of group size. Experimental Economics. 2013;18(1):4–14.

36. Boyd R, Schonmann RH, Vicente R. Hunter–Gatherer population structure and the evolution of contingent cooperation. Evol Hum Behav. 2014;35(3):219–227.

37. Barcelo H, Capraro V. Group size effect on cooperation in one-shot social dilemmas. Sci Rep. 2015;5:7937. [PMC free article] [PubMed]

38. Bowles S. Cultivation of cereals by the first farmers was not more productive than foraging. Proc Natl Acad Sci USA. 2011;108(12):4760–4765. [PMC free article] [PubMed]

39. Ferguson RB. The prehistory of war and peace in Europe and the Near East. In: Fry DP, editor. War, Peace, and Human Nature: The Convergence of Evolutionary and Cultural Views. Oxford Univ Press; Oxford: 2013. pp. 191–240.

40. O'Brien MJ, Laland KN. Genes, culture, and agriculture. Curr Anthropol. 2012;53(4):434–470.