

Geographic mosaics and changing rates of cereal domestication

Robin G. Allaby (Warwick), Chris Stevens (UCL), Leilani Lucas (UCL), Osamu Maeda (Tsukuba), Dorian Q Fuller (UCL)*

*Corresponding author: Dorian Q Fuller (University College London), d.fuller@ucl.ac.uk

Abstract

Domestication is the process by which plants or animals evolved to fit a human-managed environment, and it is marked by innovations in plant morphology and anatomy that are in turn correlated with new human behaviours and technologies for harvesting, storage and field preparation. Archaeobotanical evidence has revealed that domestication was a protracted process taking thousands of plant generations. Within this protracted process there were changes in the selection pressures for domestication traits as well as variation across a geographic mosaic of wild and cultivated populations. Quantitative data allow us to estimate the changing selection coefficients for the evolution of non-shattering (domestic-type seed dispersal) in Asian rice (*Oryza sativa* L.), barley (*Hordeum vulgare* L.), emmer wheat (*Triticum dicoccon* (Shrank) Schübl.) and einkorn wheat (*T. monococcum* L.). These data indicate that selection coefficients tended to be low, but also that there were inflection points at which selection increased considerably. For rice, selection coefficients on the order of 0.001 prior to 5500 BC shifted to > 0.003 between 5000 and 4500 BC, before falling again as the domestication process ended 4000-3500 BC. In barley and the two wheats selection was strongest between 8500 and 7500 BC. The slow start of domestication may indicate that initial selection began in the Pleistocene Glacial era.

Introduction

Domestication is the transformation of other species through interactions with humans and human-managed environments, such that the reproductive success of those species and their productivity for human-valued traits, such as food value or fibre-production, both increased [1]. This can be regarded as a form of coevolution [2-5], in which the human side of the relationship takes place primarily through cultural evolution, i.e. development of techniques and technologies of ecological management transmitted culturally, while the plants or animals evolve through normal biological evolution (genetic transmission). Both cultural innovations and evolutionary developments in plant morphology and physiology occurred through the domestication process, making both human cultivators and cultivated crops better adapted, and able to exist in increased population sizes and across a greater range of geography. This is increasingly discussed in terms of niche construction theory [4, 6, 8, 9]. Agriculture represents a major shift of biosphere systems in which human societies, and their growing populations, increasingly became a global driving force in environmental change [8-10]. Thus understanding evolutionary processes involved in domestication is not just fundamental to biology, as an example of biological evolution but also as a key transition in biosphere systems. In terms of human history, agricultural production ecologies based on domesticated species provided the basis for all historical and urban civilizations.

Despite the centrality of domestication to evolutionary studies since the time of Darwin [13], much has changed in our understanding of these processes in recent years through the accumulation of empirical evidence, including the sub-fossil record provided by archaeology and discoveries through molecular genetics [3, 14-16]. Genetic evidence makes clear that not all "domestication-related traits" were evolving during initial domestication. As such it is useful to

1
2
3 separate true domestication traits, those traits which underwent directional selection when a
4 species first entered an intensive co-evolutionary relationship with humans, from those traits
5 relating to diversification or crop improvement, that were selected subsequently to domestication,
6 and often creating geographically distinct varieties. Relating to archaeology, the growth of
7 archaeobotanical evidence has provided a sub-fossil record in which phenotypic changes relating to
8 domestication can be directly documented over time and space, allowing rates of change to be
9 estimated for different traits in different taxa and regions based on empirical evidence. The current
10 study provides an updated analysis of such data for cereal domestication, in particular in terms of
11 the trait of non-shattering ears or panicles.
12
13

14 Non-shattering ears or panicles are often regarded as the *sine qua non* feature of cereal
15 domestication, as this prevents natural seed dispersal, a process necessary in the wild, leaving
16 cereals reliant on farmers to harvest and plant their seeds [17, 18]. Recent accumulation of
17 archaeobotanical evidence has made it possible to document empirically changes in the proportions
18 of human-reliant (i.e. domesticated) cereals in past populations during the era of agricultural origins
19 for some cereals, including West Asian wheat (*Triticum monococcum* L. and *T. dicoccon* (Shrank)
20 Schübl.) and barley (*Hordeum vulgare* L.) [19-21]. Data have also become available for at least part of
21 the trajectory in Chinese rice (*Oryza sativa* L.) domestication [15, 22, 23]. Contrary to previous
22 expectations that selection through sickle harvesting should be strong leading to rapid
23 domestication, on the order of a century (20-200 years) [24-26], the archaeobotanical evidence of
24 wheat and barley indicates protracted transitions with documented change in cereal morphology
25 recorded over about 3000 years [15, 19, 27]. This indicates that the strength of selection for
26 domestication traits is orders of magnitude weaker than previously supposed [15, 28, 29]. It is also
27 plausible that selection for domestication traits was not always directional, and may have fluctuated
28 around a meta-stable equilibrium of partially non-shattering [30], maintained by periods of fallow,
29 variation in harvesting techniques and continued bolstering of human cereal stores from wild
30 populations [30, 31]. At the level of the meta-population, which included fallow fields, and feral
31 crops, as well as those under active cultivation and sympatric wild population, cereals undergoing
32 domestication may be expected to have included processes of “fluctuating selection” [32, 33].
33
34
35
36

37 Given that domestication was a protracted process there is no reason to assume that human
38 practices, ecological conditions and therefore selection pressures were constant and unchanging
39 over several millennia. To assume that selection pressures were constant implies that environmental
40 parameters, such as those relating to climate, and human behaviours were unchanging over a period
41 of millennia or 100-200 human generations. More reasonable is to accept that changing
42 environmental conditions, social conditions and technology could have all contributed to
43 accelerating or slowing down, or even reversing, selection processes on early cultivated cereals.
44 Previous attempts to estimate rates of phenotypic evolution for domestication traits and associated
45 selection coefficients, however, have assumed a single constant rate of domestication, based on
46 linear regression of data (figure 1a,b). This has produced estimates of rates of phenotypic change,
47 based on *Darwin* or *Haldane* units, that are in the same order of magnitude as estimates from
48 modern microevolutionary studies unrelated to domestication, or even on the slow side [15, 28, 34];
49 this was somewhat surprising given that it was often assumed that the anthropogenic nature of
50 domestication might lead to faster evolution [13, 24, 25]. A weakness of this approach, however, is
51 that the single estimate of evolutionary rate estimate is really an approximate average of what are
52 presumably varying rates, as selection strength varied over the course of the domestication process.
53
54
55

56 The present contribution takes the analysis of these data closer to a realistic estimate of the
57 changing rates of evolution and selection pressures over the course of a given domestication
58
59
60

1
2
3 episode. It is expected that any evolutionary process of directional selection will approximate a
4 sigmoidal (logistic) pattern of change [2, 24]. In the present contribution we explore the potential to
5 use any pair of time series data-points to represent the specific sections of the sigmoidal process,
6 more localized in space and over a shorter time scale (figure 1c). As such we are modelling from
7 archaeobotanical data - the fossil record of crop domestication - how the strength of selection
8 changed over the course of the entire domestication process, in other words, whether different
9 sigmoidal processes were in action over time. This in turn allows us to identify particular periods
10 when human-driven selection was stronger, and it also provides a baseline for estimating backwards
11 in time to when the earliest selection for domestication traits began. In other words we are able to
12 predict when the beginnings of the effects of pre-domestication activity occurred, e.g. the gathering
13 of wild grasses, as well as identifying when cereal domestication intensified.
14
15

16 **Materials and methods**

17
18 We have collected all of the available sub-fossil data for cereal non-shattering from
19 archaeological plant assemblages in the putative geographical regions of origin that indicate change
20 towards domestication traits for four crops, including Asian rice (*Oryza sativa*), barley (*Hordeum*
21 *vulgare*), einkorn wheat (*Triticum monococcum*), and emmer wheat (*Triticum dicoccon*) (ESM). In the
22 current study we have excluded indeterminate remains of wheat and barley as well as immature
23 (green-harvested) spikelet bases of rice. Previous studies have used the proportions of uncertain
24 specimens to estimate error margins and standard deviations [15, 28], whereas we have taken a
25 different approach to this to account for sample size (see below). Assemblage data are placed on an
26 absolute time scale by calculation of the median age estimate of the archaeological phases [15, 27].
27 All dates are given in calibrated BC.
28
29

30
31 These data are drawn from across multiple sites, which are taken as representative of an
32 evolutionary process of domestication taking place over a broader region and period. This assumes
33 that archaeobotanical assemblages represent a regional meta-population undergoing domestication
34 over an extended period of time. This is necessary as no one archaeological site, that has yet been
35 discovered, was occupied through the entire domestication process (~4000 years), and therefore
36 there is no single stratigraphic archive that has preserved an entire domestication process *in situ*.
37 Where single sites do demonstrate increasing domestication traits, such as the rise in domesticated
38 type rice spikelet bases during the 300-400 years of occupation at Tianluoshan, a gradual change is
39 evident, similar to those from comparisons across sites [22]. As demonstrated by numerous case
40 studies, not related to domestication, geographical mosaics of co-evolution are recurrent features of
41 evolution [35], and it can be suggested that both 'hotspots; and 'cold-spots' of selection for
42 domestication traits are likely to have occurred within the broader regions of agricultural origins [30,
43 34]. Recently, genomic studies of some crops, including barley [36], emmer [37], einkorn [38], and
44 Asian rice [39, 40], indicate that modern domesticated populations derive in part from genetic
45 diversity from numerous geographically disparate wild gene pools.
46
47

48
49 In the present analyses, time series data were modelled as selection chains, themselves
50 inferred from a parsimonious model of selection and spread, making the populations represented by
51 younger sites derivative of any older sites for which this is a plausible relationship. Selection chains
52 were constructed by assuming that data-points that are closer together in time, space and the
53 proportion of non-shattering are more likely to be part of the same trajectory. For the most part we
54 assumed that domestication is directional and therefore that increasing percentages of non-
55 shattering types are to be expected. We also considered the possibility that periods of negative
56 selection could have taken place over shorter timescales within the overall domestication episode.
57 This would be in keeping with the potential of fluctuation selection [32, 33] or a period of semi-
58
59
60

1
2
3 domestication [30]. This may have occurred during periods of fallow or changing practice, which
4 could have led to some selection chains becoming disconnected in our analysis due to falling
5 frequencies of shattering over time. These episodes of negative selection are indicted by grey arrows
6 in the figures below, and are discussed separately. Multiple potential pathways of evolution are
7 possible and this allows us to increase the number of estimates of selection pressure over time and
8 therefore look for general patterns in the strength of selection pressure.
9

10 We assume that it takes time for domesticates to spread between sites. In the case of early
11 rice domestication in the Lower Yangtze, all sites are in fairly close proximity, lying within an elliptical
12 area of approximately 65,000 km², accounting for evidence dating between 6000 and 2000 BC. By
13 contrast the greater “Fertile Crescent” of southwestern Asia is much larger and requires an elliptical
14 area of approximately 3.5 million km². In this region therefore some sites are quite distant from each
15 other, and thus it is more likely that selection chains should be inferred for sites that are reasonably
16 close to each other. In addition, material culture, such as lithic sickle typology, shows regional
17 differences across southwest Asia [27]. We therefore added an additional calculation to the
18 construction of selection chains in wheat and barley by creating a time and space matrix that
19 penalized longer distance and shorter time period inter-relationships.
20
21
22

23 This model considered two rate parameters, the rate with which frequencies change
24 between two sites, and the velocity with which cultures would be required to move between sites.
25 The rate of transition towards tough rachis dominance between sites was inferred through the tough
26 rachis allele change between two sites represented by the selection coefficient (*s*). The minimum
27 velocity (*v_m*) with which individuals would have to travel between sites in order for cultural
28 continuity to be represented is estimated by utilizing the geographical distance over the maximum
29 amount of time permitted by the archaeological dates. In the case of the Near East, the geographical
30 distance was calculated with respect to viable routes that circumvented the central desert regions of
31 the Near East by preferentially taking routes through the Fertile Crescent.
32
33

34 To calculate *s* we first had to infer the allele frequencies associated with phenotypic
35 frequencies observed in the archaeological record. To do this, we calculated the inbreeding
36 coefficient (*F*) associated with the mating system of the crops, which was assumed to be 98%
37 inbreeding. The inbreeding coefficient was determined by simulation that began with Hardy-
38 Weinberg proportions of genotypes, *P*, *R* and *Q*, (dominant homozygous, heterozygous and recessive
39 homozygous genotypes, respectively) which were then mated with a 0.98 probability of selfing. The
40 subsequent generation gave rise to new proportions of *P*, *Q* and *R* that deviated from Hardy-
41 Weinberg, the reduction in heterozygosity being an estimate of *F*. Such that
42
43

$$F = \frac{R - q^2}{pq} \quad 1$$

44 where *R* is the proportion of heterozygotes, and *p* and *q* are dominant and recessive allele
45 frequencies, respectively. Generations were iteratively produced, and *F* calculated each generation
46 until it ceased to change by more than 0.00001, indicating the simulation had converged on the
47 inbreeding equilibrium and a close approximation of *F* obtained. We assumed that tough rachis
48 phenotypes represented homozygous recessive mutations, and therefore the *Q* value of genotypes,
49 and associated with the *q* allele. Allele frequency was then determined by finding values of *q* that
50 satisfy the equation
51
52
53
54

$$Q = q^2 + Fpq \quad 2$$

where Q is the observed proportion of tough rachis grains in the archaeobotanical record. To find s we simulated phenotypes of P, R, and Q with proportions calculated from the determined allele frequencies and inbreeding coefficient beginning with the allele frequency of q associated with the oldest of a pair of archaeological sites. New generations were constructed as before, with P, R and Q genotypes mating with themselves with a 0.98 probability. Each generation the proportion of Q was modified by s such that

$$Q' = Q(1 - s) \quad 3$$

where Q' is the proportional value of Q after a round of selection. Note that s took negative values since the recessive homozygote is advantageous in this case. The simulations proceeded through a number of generations defined by the difference in age between the two archaeological sites under comparison. Values of s were then determined that coincided with the observed change in tough rachis frequency between the two archaeological sites under comparison. Simulations to calculate s values from data sets of age and tough rachis proportions were carried out by a program written by RGA (available on request). The simulations also recorded the date in generations that various frequencies would be reached ranging from 0.00001 to 1.

Selection chains were then determined from transition scores, which were calculated from the velocity of movement between sites and strength of selection. To emphasize the parsimony of slow movement and selection, the inverse of velocity and selection coefficient were used, such that a transition score (T_s) between two sites could be summarized as:

$$T_s = (1/v_m \times 1/s)^{1/2} \quad 4$$

Which is the geometric mean of the inverses. The geometric mean is relatively robust to the different orders of magnitude associated with velocity and selection coefficient values, consequently in this model they are of equable influence on the transition score. Each archaeological locality had a series of transition scores relating to the other sites, and the highest scoring values were taken as the most likely connections of cultural continuity explained by a combination of the least selection and minimum travel speed required. However, under this model older sites will tend to become favoured over younger sites as likely points of cultural connection to later sites, even if associated with a stronger selection pressure, because of their tendency to be associated with lower velocities. To account for this we envisioned the possibility that sites could have existed over a longer time frame than the absolute dates suggest in the model and imputed a velocity that assumes all sites to be contemporaneous. In such a case the strength of selection is unaffected, since we are inferring what the frequency would have been at a particular time point, but the value s remains unchanged over time. The imputed minimum velocity (v_{mi}) was calculated as:

$$v_{mi} = d/c \quad 5$$

Where d and c are the distance between sites and a constant, respectively, for which we used an arbitrary value of 2000. Consequently the imputed transition score (T_{si}) was calculated as in equation 4, with v_i substituted for v_{mi} . Note that our choice of c has no effect on the relative magnitudes of T_{si} values because of the robustness of the geometric mean to differences in scale between terms.

Selection chains were then established by inferring most likely connections between sites based on the highest transition scores. We found that imputed transition scores down-weighted the influence of the oldest sites but made little difference to later connections between sites.

1
2
3 Selection chains defined which selection coefficients that had been calculated between
4 archaeological sites should be retained. Ranges for selection coefficient values were generated by
5 considering the 95% and 67% ranges of tough rachis proportions at sites, for their given sample sizes.
6 These were obtained using the Beta distribution, with parameters α and β defined as the counts of
7 tough rachis and wild type rachis plus one, respectively. The pairs of proportions for each site were
8 then used to calculate values of s using the same program as above, highest and lowest values were
9 taken as the range limits for 95% and 67%, respectively, and their associated age dates.
10

11 The selection chains were then used to determine which selection coefficients were
12 associated with the domestication process, and particularly the earliest stages of the process. These
13 had to be taken from tough rachis frequency values above zero found at the oldest archaeological
14 sites, since in effect the true proportions at these sites is unknown. The earliest selection coefficients
15 were then used to estimate an average early selection coefficient. This value was then fed into the
16 previous simulation as a fixed parameter to determine the ages at which various allele frequencies
17 would be reached, given the allele frequency of a given site at a given time. We assumed a starting
18 frequency for a new mutation to be 0.00001 (0.001%), which assumes an effective population size of
19 50,000, not unreasonable for cereals given genetic diversity estimates. However, ages associated
20 with possible higher starting frequencies were also recorded.
21
22
23
24
25

26 Results

27
28 **Rice**, *Oryza sativa*, has long been a major staple of civilizations in East, South and Southeast
29 Asia. Recent genomic data strongly support domestication of subspecies *japonica* from perennial
30 *Oryza rufipogon*, with the closest living wild populations found in southern China [41, 42]. However,
31 former wild populations in central China extirpated over the last 1000 years are likely to be closer to
32 the ancestor (figure 2a). Domesticated rice arrived at Shixia in Guangdong at ca. 2600 BC [43]. Other
33 Asian rice subspecies, notably subspecies *indica* and the *aus* group, have distinct geographical origins
34 [40, 42, 44]. Archaeobotanical data points to the earliest rice cultivation in the Yangtze basin, with
35 two candidate regions around the Middle and Lower Yangtze basin having the greatest support from
36 current archaeobotanical data [23, 45]. While selection for non-shattering may have begun in more
37 than one part of the Yangtze and its tributaries the most completely documented domestication is
38 that of the Lower Yangtze.
39
40

41 Rice domestication in the Lower Yangtze is represented by a clear archaeological sequence
42 of assemblages that show growing proportions of non-shattering spikelet bases (figure 1b; figure 2b),
43 rising from less than 15% at ca. 5700 BC to 46.7% a millennium later. After this period we have the
44 potential of divergent selection paths into later periods (figure 2b). Given that some subsequent
45 sites have lower percentages, such as Liangzhu and sites in the Yellow River, it is possible that these
46 represent dispersal northwards starting from populations in which this domestication trait is not yet
47 fixed and that began dispersing northwards prior to the occupation of Caoxieshan. Allowing
48 fluctuations of negative selection, however, provides a better explanation, for the reduction in non-
49 shattering in the later phases of Maoshan phases, and for deriving the Sushui (Yangshao) from
50 Caoxieshan (table S3). These periods of selection reversal make sense as increased irrigation [46],
51 would have provided habitat for wild or weedy rice.
52
53
54

55 Taking the Tianluoshan-Caoxieshan selection chain the maximum selection coefficient
56 reaches nearly 0.003 in the early 5th millennium BC (figure 2c). Taking 500-year bin averages places a
57 peak selection strength at ~ 0.0033 at ca. 4750 BC, with selection strength declines thereafter. This
58
59
60

1
2
3
4 corresponds to the inferences that Tianluoshan records a key tipping point in the Lower Yangtze
5 domestication process of rice, with weaker selection under pre-domestication cultivation before this
6 period, and slowing selection as the domestication process finished shortly after 4000 BC [22, 40].
7 Based on our new calculations we estimate that non-shattering would have been as low as 0.00001
8 between 12,714-13,361 years before present (table S2, S13).

9
10 **Barley**, *Hordeum vulgare*, was domesticated in Southwest Asia (figure 3a), drawing from
11 geographically widely dispersed wild populations [36]. It is the best documented of the Near Eastern
12 cereals in terms of the number and size of archaeobotanical rachis assemblages, which indicate
13 almost purely wild-type, fully shattering populations before 9500 BC, with the gradual appearance of
14 non-shattering rachides, rising to as much as 30% in a few assemblages, between 9000 and 8500 BC
15 [27, 21]. After 7400 cal. BC some sites show apparently fixed, 100% non-shattering barley. As barley
16 is widespread, occurring in all parts of the Fertile Crescent, data likely represent multiple regional
17 domestication chains, and in accordance with this we find several probable distinct selection chains
18 (figure 3b). We also checked potential negative selection fluctuations, but none of these had
19 transition scores as high as for positive selection indicating that they are less likely than the positive
20 selection chains (table S6). Barley selection coefficients increase from < 0.002 to > 0.003 between
21 the early and late 9th millennium BC, with stronger selection (> 0.005) estimated for the Northern
22 Levant (figure 3c). Selection coefficients appear to decrease from the later 8th millennium BC. Based
23 on our new calculations we estimate that non-shattering would have been as low as 0.00001
24 between 10,405 and 10,705 BC in the Northern Levant (based on Jerf el Ahmar), but between 17,881
25 and 21,792 BC, average ca. 19,996 BC in the Southern Levant (based on similar estimates from
26 several early sites: table S5, S13). There is some support in the data for two discernible barley
27 domestications occurring in the Southern Levant, which are picked out by the selection chains
28 associated with the Netiv Hagdud and Zahrat Adh-Dhra lineages.

29
30 **Emmer**, *Triticum dicoccon* derives from wild populations in the Fertile Crescent (figure 4a).
31 There are fewer studied and quantified assemblages of spikelet fork material from this species, with
32 a total identifiable sample size of only 672. The earlier assemblages, up to 8300 BC, are all from the
33 Southern Levant, and demonstrate ~26% non-shattering, with later assemblages from the north and
34 east. Nevertheless our spatio-temporal heatmap (figure S5) indicates the likelihood of at least two
35 selection chains in emmer (figure 4b). We tested for potential negative selection events, but none
36 are likely (table S9) At 8000 BC selection is close to the ~0.001 level that is typical of many of our
37 estimates across crops. Although limited, data from northern and eastern sites may indicate an
38 increase in selection on emmer shattering to > 0.004 in the 7th millennium BC. Based on our
39 calculations we estimate the origins of selection, i.e. non-shattering at 0.00001, occurred between
40 18,346 and 25,606, with older part of this range favoured by the Southern Levant evidence (table S8,
41 S13).

42
43 **Einkorn**, *Triticum monococcum* derives from wild populations with a more northerly
44 distribution than emmer, and most of our data comes from northern Fertile Crescent sites, although
45 einkorn reached at least as far south as Tell Qarassa (figure 4a). The total number of rachis remains
46 is quite low ($n=504$), and the earliest site, Tell Qaramel, has surprisingly high levels of non-shattering,
47 ~22%, prior to 10,000 BC, although dates have wide error margins and could be up to 1000 years
48 later [27, 29]. Later sites, including Jerf el Ahmar and Dja'de, appear to be entirely shattering,
49 although cultivation is indicated at these sites by other lines of evidence [47]. This leads us to infer
50 the main trajectory to domestication may not have involved this pair of sites (figure 4d). Setting
51 aside those sites, the data indicate a coefficient s of ~0.001 up to 8250 BC which rises to ~0.003 after
52 8000 BC and a subsequent reduction in pressure (figure 4c). Çatal Höyük is best explained in our
53
54
55
56
57
58
59
60

1
2
3 model as a result of a loss of selection after Çafar Höyük (table S12). The levels of non-shattering
4 reached at Qaramel lead to the inference of starting frequencies of 0.00001 pure wild (shattering)
5 einkorn at ~30,000 BC, although estimates from later parts of the domestication chains provide start
6 dates between ~14,000 and ~10,000 BC (table S11, S13).
7
8
9

10 Discussion and Conclusions

11 The evidence presented in this study supports the notion that the process of domestication
12 was a slow evolutionary process. In general the selection coefficients recovered from this study
13 corroborate the low values previously calculated for cereals using alternative methodologies [28],
14 but contrast with later estimates [15].
15
16

17 An obvious question is why such low magnitudes for selection are seen within the
18 archaeobotanical data when field experiments have demonstrated that higher rates would have
19 been possible [24]? This study goes part way to addressing this question by separating out the
20 strength of selection over time. A discernible change in the strength of selection occurs around 8000
21 BC in the Near Eastern cereals, which appears coincident with the rise of lithic technologies [27]. This
22 shift in the strength of selection appears greatest in the Northern Levant, where a steep rise in
23 selection coefficients is observed alongside the increase in group 3 and 4 sickle technologies [27].
24 Interestingly, the Southern Levant cultures do not appear to increase selection strength over time,
25 implying a distinct difference in cultural practice between the two groups. Therefore, this study
26 shows that different cultural practices led to different selection regimes that perhaps were not
27 reflected in the one model system of field experiments. A second dimension to the strength of
28 selection is in the amount of selection a population can endure. Selection comes at a cost, and while
29 just a single trait that is under simple genetic control was considered in this study, in reality a
30 number of genes would have been simultaneously under selection during the domestication process.
31 An increasing number of genes under selection require that selection be proportionately weaker
32 across loci, and the values of s found in this study tally close with expectations of a selection the cost
33 model for the dozens of genes expected to have been affected by domestication [48].
34
35
36
37

38 A natural corollary of the observation that selection was weak and slow is that it is likely that
39 the selective processes driving crops down the domestication evolution trajectory extended back in
40 time beyond our currently accepted dates for the first appearance of domesticated phenotypes. The
41 assumed starting frequency in this study for a tough rachis mutant is ten-fold higher than previous
42 studies [49], so provide a conservative estimate with regard to time depth for the onset of selection.
43 Our findings are in line with previous archaeobotanical evidence that has suggested an early onset of
44 cultivation practices in the Pleistocene at Ohalo II in the Near East [50] and in the Yangtze valley by
45 the end of the Pleistocene or earliest Holocene [51,52]. The variable nature of the climate during this
46 time period is likely to have led to dead ends as settlements and ways of life were abandoned. This is
47 likely the case for Ohalo II, which appears to be associated with an independent selection chain to
48 the studies included here. Similarly, even within the Holocene epoch the selection chains established
49 in our model suggest that the Netiv Hagdud associated chains ultimately died out in favour of the
50 ZAD2 associated chain for barley.
51
52

53 The complexity of these domestications, with varying strengths of selection at different
54 points of time and across distinct geographical regions, suggests a number of different processes in
55 action. The selection chains identify this structure in the data. The clearest separation occurs
56 between northern and southern cultures in the Levant, and the Lujijajiao and Tianluoshan associated
57
58
59
60

1
2
3 cultural lineages in the Lower Yangtze. In the case of emmer wheat these seem to reflect
4 independent domestication events, and even within the Southern Levant there is evidence of two
5 separate lineages that may reflect parallel rises of domesticate forms.
6

7 The nature of the selective agents driving crops down the domestication trajectory further
8 back into the Late Pleistocene is currently a matter of speculation. It may be the case that direct
9 cultivation was not at all involved, and that the signal we detect is associated with more ancient
10 impacts on the ecology surrounding humans before the late glacial maximum. Such impacts could
11 have been harvesting or gathering pressures in the wild which simply reduced the strength of wild-
12 type dispersal adaptations. However, such weak selection pressures require substantially large
13 population sizes to counter the effects of drift. Consequently, the effects we detect should have
14 been systematic and widespread, requiring a significant number of agents to apply the pressures
15 involved. If the selection pressures were derived from quite simple human disturbances of the
16 ecology around them such as might be associated with a natural herbivore community, then it may
17 be the case that the time depth of signal we observe may relate a period in time in which sufficient
18 population densities had been reached in the Levant and Yangtze regions, respectively.
19
20
21
22

23 Acknowledgements

24
25 Research and writing on this paper by DQF, LL and CJS, has been carried out as part of the
26 Comparative Pathways to Agriculture project, supported by an Advanced Investigator Grant from the
27 ERC (no. 323842).
28
29
30

31 References

- 32
33
34
35 1. Larson G., Piperno D. R., Allaby R. G., Puruggan M. D., Andersson L., Arroyo-Kalin M. et al.
36 2014 Current perspectives and the future of domestication studies. *Proc. Natl. Acad. Sci. USA*
37 **111(17)**, 6139–46 (doi: 10.1073/pnas.1323964111).
38
39 2. Rindos D. 1984 *The Origins of Agriculture. An Evolutionary Perspective*. London: Academic
40 Press.
41
42 3. Purugganan M. D, Fuller D. Q. 2009 The nature of selection during plant domestication.
43 *Nature* **457(7231)**: 843-848 (doi: 10.1038/nature07895).
44
45 4. Zeder M. A. 2015 Core questions in domestication research. *Proc. Natl. Acad. Sci. USA*
46 **112(11)**, 3191-3198 (doi: 10.1073/pnas.1501711112)
47
48 5. Allaby R. G., Kistler L., Gutaker R. M., Ware, R. Kitchen J. L., Smith, O. Clarke A. C. 2015
49 Archaeogenomic insights into the adaptation of plants to the human environment: pushing
50 plant–hominin co-evolution back to the pliocene. *J Hum Evol.* **79**, 150-7 (doi:
51 10.1016/j.jhevol.2014.10.014)
52
53 6. Smith B. D. 2011 General patterns of niche construction and the management of wild plant
54 and animal resources by small-scale pre-industrial societies. *Phil. Trans. R. Soc. B* **366**, 836–
55 848 (doi: 10.1098/rstb.2010.0253)
56
57
58
59
60

- 1
2
3
4 7. Smith B. D. 2015 A comparison of Niche Construction Theory and Diet Breadth Models as
5 explanatory frameworks for the initial domestication of plants and animals. *J. Archaeol. Res.*
6 **23(3)**, 215-262 (doi/10.1007/s10814-015-9081-4)
7
- 8
9 8. Ellis E. C. 2015 Ecology in an anthropogenic biosphere. *Ecol. Monogr.* **85(3)**, 287-331 (doi:
10 10.1890/14-2274.1)
11
- 12 9. Boivin N. L., Zeder M.A., Fuller D. Q, Crowther A., Larson G., Erlandson J. M., Denham T.,
13 Petraglia M. D. 2016 Ecological consequences of human niche construction: Examining long-
14 term anthropogenic shaping of global species distributions. *Proc. Natl. Acad. Sci. USA*
15 **113(23)**, 6388–6396 (doi: 10.1073/pnas.1525200113)
16
- 17 10. Ruddiman W. F, Fuller D. Q, Kutzbach J. E., Tzedakis P. C., Kaplan J. O. , Ellis E. C. et al. 2016
18 Late Holocene climate: Natural or anthropogenic? *Rev. Geophys.* **54**, 93-118. (doi:
19 10.1002/2015RG000503)
20
- 21 22 11. Kareiva P., Watts S., McDonald R., Boucher T. 2007 Domesticated nature: Shaping
23 landscapes and ecosystems for human welfare. *Science* **316(5833)**, 1866-1869. (doi:
24 10.1126/science.1140170).
25
- 26 27 12. Jackson S. T., Hobbs R. J. 2009 Ecological restoration in the light of ecological history. *Science*
28 **325(5940)**, 567-569 (doi: 10.1126/science.1172977).
29
- 30 31 13. Darwin C. 1868. *The Variation of Animals and Plants under Domestication*. London: John
32 Murray.
33
- 34 35 14. Meyer R. S, Purugganan M. D. 2013. Evolution of crop species: genetics of domestication and
36 diversification. *Nature Rev. Genet.* **14**, 840-852 (doi:10.1038/nrg3605)
37
- 38 39 15. Fuller D. Q, Denham T., Arroyo-Kalina M., Lucas L., Stevens C. J., Qin L., Allaby R. G.,
40 Purugganan M. D. 2014 Convergent evolution and parallelism in plant domestication
41 revealed by an expanding archaeological record. *Proc. Natl. Acad. Sci. USA* **111(17)**, 6147-
42 6152 (doi/10.1073/pnas.1308937110)
43
- 44 45 16. Larson G., Fuller D. Q. 2014 The evolution of animal domestication *Annu. Rev. Ecol. Evol. Syst.*
46 **(2014)45**, 115-136. (doi: 10.1146/annurev-ecolsys-110512-135813)
47
- 48 49 17. Zohary D. 1969 The progenitors of wheat and barley in relation to domestication and
50 agricultural dispersal in the Old World. In *The domestication and exploitation of plants and*
51 *animals* (eds Ucko, P. J., Dibbleby, G. W.), pp. 47- 66. London: Duckworth.
52
- 53 54 18. Harlan J. R, De Wet J. M. J, Price E. G. 1973 Comparative evolution of cereals, *Evolution* **27**,
55 311-325 (doi: 10.2307/2406971).
56
- 57 58 19. Tanno K-I., Willcox G. 2012. Distinguishing wild and domestic wheat and barley spikelets
59 from early Holocene sites in the Near East. *Veg. Hist. Archaeobot.* **21(2)**, 107-115
60 (doi:10.1007/s00334-011-0316-0)

- 1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
20. Weide A., Riehl S., Zeidi M., Conard N. J. 2015 Using new morphological criteria to identify domesticated emmer wheat at the aceramic Neolithic site of Chogha Golan (Iran). *J Archaeol. Sci.* **57**, 109-118 (doi: 10.1016/j.jas.2015.01.013)
 21. Arranz-Otaegui A., Colledge S., Zapata L., Teira-Mayolini L. C., Ibáñez J. J. 2016 Regional diversity on the timing for the initial appearance of cereal cultivation and domestication in southwest Asia. *Proc. Natl. Acad. Sci. USA* **113(49)**, 14001-14006. (doi: 10.1073/pnas.1612797113)
 22. Fuller D. Q, Qin L., Zheng Y., Zhao Z., Chen X., Hosoya L. A. Sun G. P. 2009 The domestication process and domestication rate in rice: Spikelet bases from the Lower Yangtze. *Science* **323(5921)**, 1607-1610 (doi: 10.1126/science.1166605)
 23. Deng ZH., Qin L., Gao Y., Weisskopf A., Zhang C. Fuller D. Q. 2015 From early domesticated rice of the Middle Yangtze Basin to millet, rice and wheat agriculture: archaeobotanical macro-remains from Baligang, Nanyang Basin, central China (6700–500 BC). *PLoS One* **10(10)**, e0139885. (doi:10.1371/journal.pone.0139885)
 24. Hillman G. C., Davies M. S. 1990 Domestication rates in wild-type wheats and barley under primitive cultivation. *Biol. J. Linn. Soc.* **39(1)**, 39-78. (doi:10.1111/j.1095-8312.1990.tb01611.x)
 25. Harlan, J. R. 1992 *Crops and Man*. 2nd Edition. Madison WI, American Society for Agronomy.
 26. Zohary D. 2004 Unconscious selection and the evolution of domesticated plants. *Econ. Bot.* **58(1)**, 5-10 (doi:10.1663/0013-0001(2004)058[0005:USATEO]2.0.CO;2)
 27. Maeda O., Lucas L., Silva F., Tanno K-I, Fuller D. Q. 2016 Narrowing the harvest: Increasing sickle investment and the rise of domesticated cereal agriculture in the Fertile Crescent. *Quat. Sci. Rev.* **145**, 226-237 (doi:10.1016/j.quascirev.2016.05.032)
 28. Purugganan M. D, Fuller D. Q. 2011 Archaeological data reveal slow rates of evolution during plant domestication. *Evolution* **65(1)**, 171-183 (doi:10.1111/j.1558-5646.2010.01093.x)
 29. Fuller D. Q, Willcox G., Allaby R. G. 2012. Early agricultural pathways: moving outside the 'core area' hypothesis in Southwest Asia. *J. Exp. Bot.* **63(2)**, 617-633. (doi: 10.1093/jxb/err307)
 30. Fuller D. Q., Allaby R. G., Stevens C. 2010. Domestication as innovation: the entanglement of techniques, technology and chance in the domestication of cereal crops. *World Archaeol.* **42(1)**, 13-28 (doi: 10.1080/004382409034296800).
 31. Willcox G. 1999. Agrarian change and the beginnings of cultivation in the Near East: evidence from wild progenitors, experimental cultivation and archaeobotanical data. In *The prehistory of food. Appetites for change* (Gosden C, Hather J, eds.). London: Routledge, 478–500.
 32. Bell, G. 2010. Fluctuating selection: the perpetual renewal of adaptation in variable environments. *Phil. Trans. Roy. Soc. B* **365(1537)**, 87 - 97.

- 1
2
3 33. Thompson J. N. 2013. *Relentless Evolution*. Chicago, IL: University of Chicago Press.
4
5
6 34. Fuller D. Q, Asouti E., Purugganan M. D. 2012 Cultivation as slow evolutionary entanglement:
7 comparative data on rate and sequence of domestication. *Veg. Hist. Archaeobot.* **21(2)**, 131-
8 145. (doi: 10.1007/s00334-011-0329-8)
9
10 35. Thompson J. N. 2005. *The Geographic Mosaic of Coevolution*. Chicago, IL: University of
11 Chicago Press.
12
13 36. Poets A. M, Fang Z., Clegg M. T., Morrell P. 2015 Barley landraces are characterized by
14 geographically heterogeneous genomic origins. *Genome Biol.* **16**, 173. (doi: 10.1186/s13059-
15 015-0712-3)
16
17 37. Civián P, Ivaničová Z., Brown T. A. 2013 Reticulated origin of domesticated emmer wheat
18 supports a dynamic model for the emergence of agriculture in the Fertile Crescent. *PLoS One*
19 **8(11)**, e81955. (doi: 10.1371/journal.pone.0081955).
20
21
22 38. Kilian B, Özkan, H., Walther A., Kohl J., Dagan T., Salamini F., Martin W. 2007 Molecular
23 diversity at 18 loci in 321 wild and 92 domesticate lines reveal no reduction of nucleotide
24 diversity during *Triticum monococcum* (einkorn) domestication: Implications for the origin of
25 agriculture. *Mol. Biol. Evol.* **24(12)**, 2657-2668. (doi: 10.1093/molbev/msm192)
26
27 39. Londo J. P., Chiang YC, Hung KH, Chiang TY, Schaal B. A. 2006 Phylogeography of Asian wild
28 rice, *Oryza rufipogon*, reveals multiple independent domestications of cultivated rice, *Oryza*
29 *sativa*. *Proc. Natl. Acad. Sci. USA* **113(49)**, 9578–9583. (doi: 10.1073/pnas.0603152103).
30
31
32
33 40. Civián P., Craig H, Cymon J, Brown TA. 2015 Three geographically separate domestications of
34 Asian rice. *Nature Plants* **1**, 15164. (doi: 10.5281/zenodo.20740)
35
36
37 41. Huang XH, Kurata N, Wei XH, Wang ZX, Wang A, Zhao Q et al. 2012 A map of rice genome
38 variation reveals the origin of cultivated rice. *Nature* **490(7421)**, 497-501.
39 (doi:10.1038/nature11532)
40
41 42. Choi JY, Platts A. E., Fuller D. Q, Hsing Y-L., Wing R. A., Purugganan, M. D. 2017 The Rice
42 Paradox: Multiple Origins but Single Domestication in Asian Rice. *Mol Biol Evol.* **2017**,
43 msx049. (doi: 10.1093/molbev/msx049)
44
45 43. Yang XY, Wang WW, Zhuang YJ, Zhao L, Ma ZK, Ma YC, Cui Y, Wei J, Fuller D. Q. 2016 New
46 radiocarbon evidence on early rice consumption and farming in South China. *Holocene* **2016**,
47 1-7 (doi: 10.1177/0959683616678465)
48
49 44. Fuller D. Q, Sato Y. I., Castillo C., Qin L., Weisskopf A. R. , Kingwell-Banham E. J., et al. 2010.
50 Consilience of genetics and archaeobotany in the entangled history of rice. *Archaeol.*
51 *Anthropol. Sci.* **2**, 115-131. (doi: 10.1007/s12520-010-0035-y)
52
53 45. Silva F., Stevens C. J., Weisskopf A., Castillo C., Qin L., Bevan A., Fuller D. Q. 2015. Modelling
54 the geographical origin of rice cultivation in Asia using the Rice Archaeological Database.
55 *PLoS One* **10(9)**, e0137024. (doi: 10.1371/journal.pone.0137024)
56
57
58
59
60

- 1
2
3 46. Weisskopf A., Qin L., Ding J., Ding P., Sun G., Fuller D. Q. 2015 Phytoliths and rice: from wet
4 to dry and back again in the Neolithic Lower Yangtze. *Antiquity* **89 (347)**, 1051-1063
5
6 47. Willcox G., Fornite S., Herveux L. 2008 Early Holocene cultivation before domestication in
7 northern Syria. *Veget Hist Archaeobot* **17(3)**, 313-325
8
9 48. Allaby R.G., Kitchen J. L., Fuller D. Q. 2016 Surprisingly low limits of selection in plant
10 domestication. *Evol. Bioinform.* **11(S2)**, 41-51 (doi: 10.4137/EBO.S33495).
11
12 49. Ladizinsky G. 1998. *Plant Evolution under Domestication*. New York NY: Kluwer Academic
13 Publishers.
14
15 50. Snir A., Nadel D., Groman-Yaroslavski I., Melamed Y., Sternberg M., Bar-Yosef O., et al. 2015
16 The origin of cultivation and proto-weeds, long before Neolithic farming. *PLoS One* **10(7)**,
17 e0131422. (doi:10.1371/journal.pone.0131422).
18
19 51. Zhijun, Z., 1998. The Middle Yangtze region in China is one place where rice was
20 domesticated: phytolith evidence from the Diaotonghuan Cave, Northern Jiangxi. *Antiquity*
21 **72 (278)**, .885-897.
22
23 52. Ma, Y., Yang X., Huan X., Wang W., Ma Z., Li Z., et al. 2016 Rice bulliform phytoliths reveal
24 the process of rice domestication in the Neolithic Lower Yangtze River region. *Quaternary*
25 *International* **426**: 126-132.
26
27 53. Fang Z., Gonzales A. M., Clegg M. T., Smith K. P., Muehlbauer G. J., Steffenson B. J., Morelle P.
28 L. 2014 Two genomic regions contribute disproportionately to geographic differentiation in
29 wild barley. *Genes Genomes Genetics* **4(7)**, 1193-1203. (doi: 10.1534/g3.114.01056).
30
31
32
33
34
35
36

Figures

37
38 **Figure 1.** Models of domestication rate and rate estimates. **A.** Hypothetical series of
39 archaeobotanical data for non-shattering plotted against time with a least squares linear regression
40 as an estimate of rate of change [15, 28, 29]. **B.** The example of rice spikelet bases from the Lower
41 Yangtze and later northern China (n=30,912), data points numbered by sites in Figure 2A (data:
42 table S1). **C.** Hypothetical series of archaeobotanical data points forming selection chains fit to
43 closest logistic curves of differing rates (method developed in this paper).
44
45
46

47
48 **Figure 2.** The evidence for the evolution of non-shattering Asian rice (*Oryza sativa*). **A.** Map of
49 evidence for rice domestication, indicating wild populations [44], and archaeological sites with
50 spikelet base data, and additional sites: 1. Sushui valley, 2. Chengyao, 3. Baligang, 4. Shixia, 5.
51 Caoxieshan, 6. Liangzhu, 7. Maoshan, 8. Kuahuqiao, 9. Lujiajiao, 10. Majiabang, 11. Xiaodouli, 12.
52 Tianluoshan. **B.** Selection chains for rice taking into account Lower Yangtze and central Chinese finds;
53 negative selection events in grey. **C.** Estimated selection coefficients (*s*) for different links in the
54 selection chains in B, and averages in 500-year bins; TL= Tianluoshan chain; Lu= Lujiajiao chain; Ca=
55 Caoxieshan chain.
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Figure 3. The evidence for the evolution of non-shattering in barley (*Hordeum vulgare*). **A.** Map of evidence for barley domestication, indicating distribution of wild populations [53], and archaeological sites with rachis remains; sites numbered: 1. Çatalhöyük, 2. Dja'de, 3. Jerf el-Ahmar, 4. Ain el-Kerkh, 5. Mureybet, 6. Abu Hureyra, 7. El Kowm 2, 8. Ramad, 9. Aswad, 10. Tell Qarassa, 11. Iraq ed-Dubb, 12. Netiv Hagdud, 13. Zahrat Adh-Dhra, 14. El-Hemmeh, 15. Wadi Fidan A, 16. Wadi Fidan C, 17. Jilat 7 and 13, 18. Azraq 31, 19. Salat Cami Yani, 20. Seker al-Aheimar, 21. Mazgaliyeh, 22. Chogha Golan, 23. East Chia Sabz. **B.** Selection chains for barley. **C.** Estimated selection coefficients (s) for different links in the selection chains in B, indicating southern and northern averages for 500 year bins.

Figure 4. The evidence for the evolution of non-shattering in wheats. **A.** Map of evidence for wheat domestication, indicating the distribution of wild *Triticum dicoccoides* [37], wild *T. boeoticum* [38], and archaeological sites with spikelet base remains; sites numbered: 1. Çatalhöyük, 2. Çaffer Höyük, 3. Nevali Cori, 4. Ail el-Kherkh, 5. Tell Qaramel, 6. Dja'de, 7. Jerf el Ahmar, 8. El Kowm 2, 9. Aswad, 10. Tell Qarassa, 11. Netiv Hagdud, 12. El-Hemmeh, 13. Salat Cemi Yani, 14. Seker al-Aheimar, 15. Chogha Golan. **B.** Selection chains for emmer and einkorn wheat, negative selection shown in grey in the case of einkorn. **C.** Estimated selection coefficients (s) for emmer and einkorn wheats, showing averages in 500 year bins. **D.** Selection chains for einkorn wheat

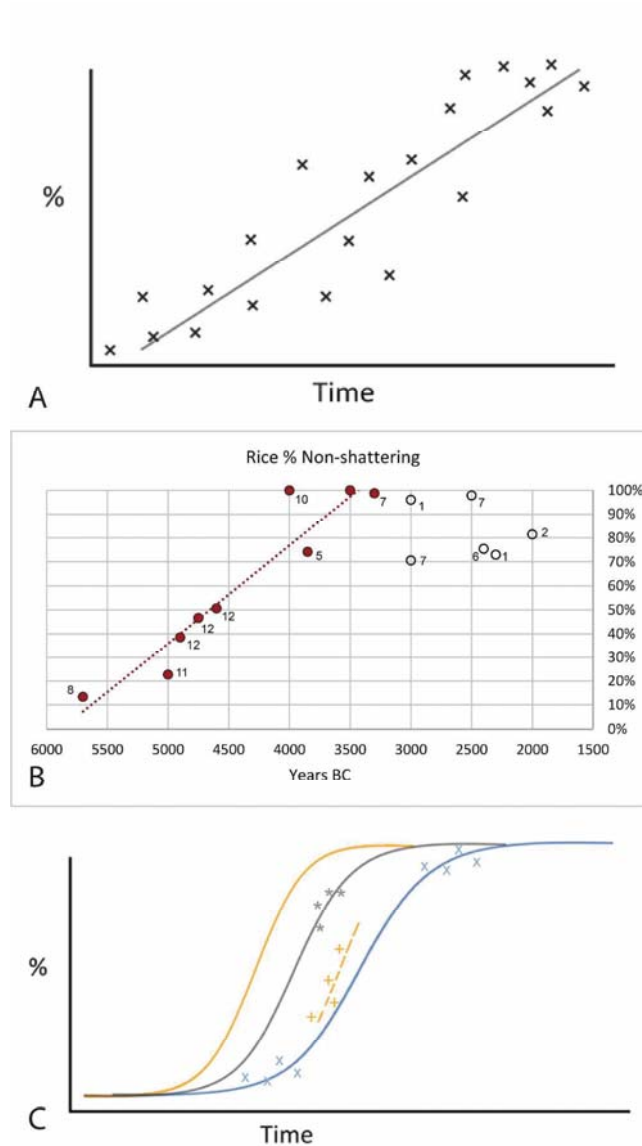


Figure 1. Models of domestication rate and rate estimates. A. Hypothetical series of archaeobotanical data for non-shattering plotted against time with a least squares linear regression as an estimate of rate of change [15, 28, 29]. B. The example of rice spikelet bases from the Lower Yangtze and later northern China (n=30,912), data points numbered by sites in Figure 2A (data: table S1). C. Hypothetical series of archaeobotanical data points forming selection chains fit to closest logistic curves of differing rates (method developed in this paper).

182x298mm (300 x 300 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

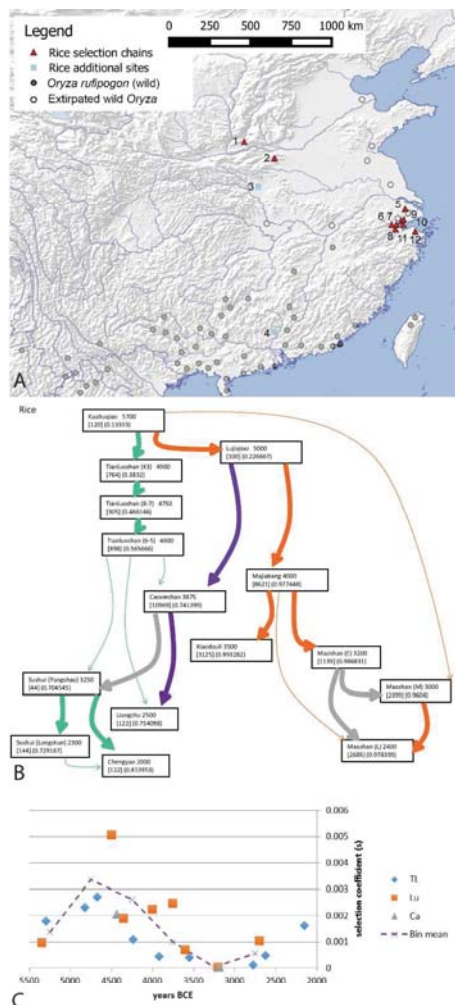


Figure 2. The evidence for the evolution of non-shattering Asian rice (*Oryza sativa*). A. Map of evidence for rice domestication, indicating wild populations [44], and archaeological sites with spikelet base data, and additional sites: 1. Sushui valley, 2. Chengyao, 3. Baligang, 4. Shixia, 5. Caoxieshan, 6. Liangzhu, 7. Maoshan, 8. Kuahuqiao, 9. Lujiajiao, 10. Majiabang, 11. Xiaodouli, 12. Tianluoshan. B. Selection chains for rice taking into account Lower Yangtze and central Chinese finds; negative selection events in grey. C. Estimated selection coefficients (s) for different links in the selection chains in B, and averages in 500-year bins; TL= Tianluoshan chain; Lu= Lujiajiao chain; Ca= Caoxieshan chain.

264x689mm (300 x 300 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

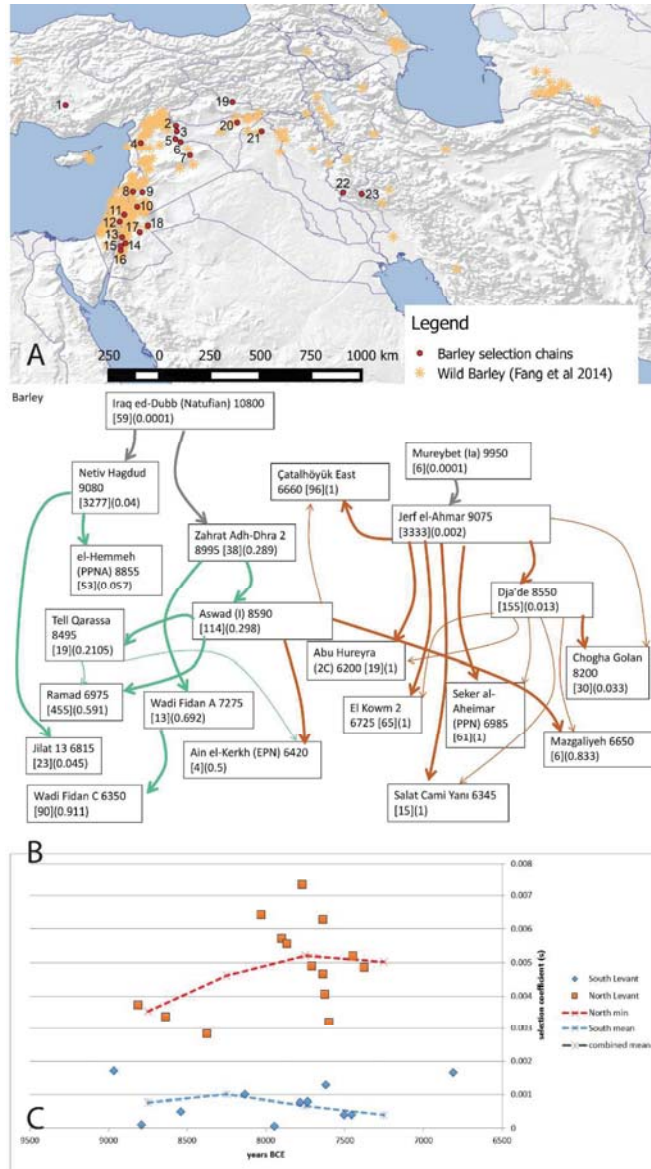


Figure 3. The evidence for the evolution of non-shattering in barley (*Hordeum vulgare*). A. Map of evidence for barley domestication, indicating distribution of wild populations [53], and archaeological sites with rachis remains; sites numbered: 1. Çatalhöyük, 2. Dja'de, 3. Jerf el-Ahmar, 4. Ain el-Kerkh, 5. Mureybet, 6. Abu Hureyra, 7. El Kowm 2, 8. Ramad, 9. Aswad, 10. Tell Qarassa, 11. Iraq ed-Dubb, 12. Netiv Hagdud, 13. Zahrat Adh-Dhra, 14. El-Hemmeh, 15. Wadi Fidan A, 16. Wadi Fidan C, 17. Jilat 7 and 13, 18. Azraq 31, 19. Salat Cami Yani, 20. Seker al-Aheimar, 21. Mazgaliyeh, 22. Chogha Golan, 23. East Chia Sabz. B. Selection chains for barley. C. Estimated selection coefficients (s) for different links in the selection chains in B, indicating southern and northern averages for 500-year bins.

181x323mm (300 x 300 DPI)

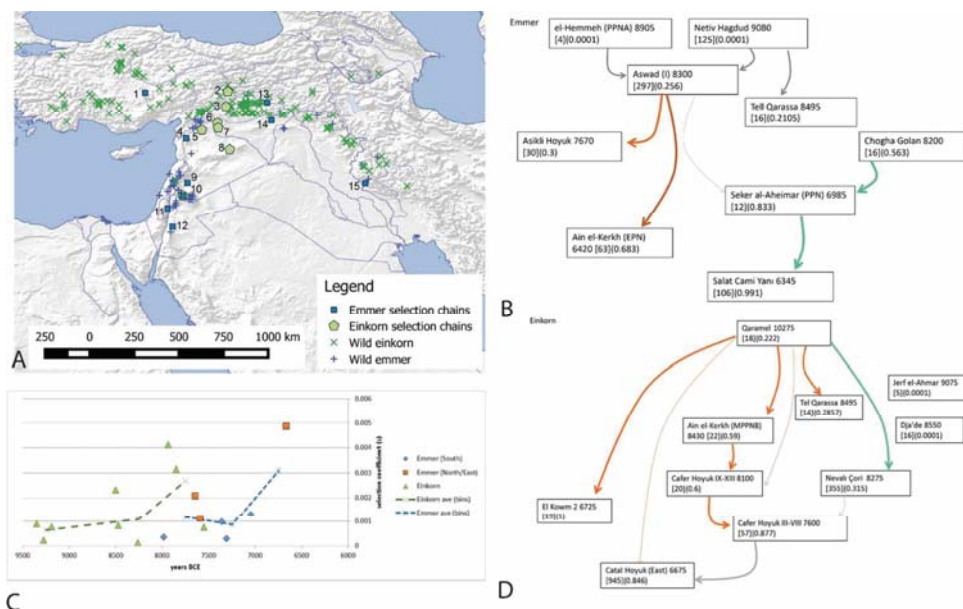


Figure 4. The evidence for the evolution of non-shattering in wheats. A. Map of evidence for wheat domestication, indicating the distribution of wild *Triticum dicoccoides* [37], wild *T. boeoticum* [38], and archaeological sites with spikelet base remains; sites numbered: 1. Çatalhöyük, 2. Çafar Höyük, 3. Nevalı Cori, 4. Ail el-Kherkh, 5. Tell Qaramel, 6. DJa'de, 7. Jerf el Ahmar, 8. El Kowm 2, 9. Aswad, 10. Tell Qarassa, 11. Netiv Hagdud, 12. El-Hemmeh, 13. Salat Cemi Yani, 14. Seker al-Aheimar, 15. Chogha Golan. B. Selection chains for emmer and einkorn wheat, negative selection shown in grey in the case of einkorn. C. Estimated selection coefficients (s) for emmer and einkorn wheats, showing averages in 500 year bins. D. Selection chains for einkorn wheat

121x75mm (300 x 300 DPI)