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Contrasting diachronic regional trends in cereal grain evolution across Eurasia: a metadata analysis of linear morphometrics from the ninth millennium BCE to today

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Abstract

The domestication of grain crops is among the most important phenomena to facilitate humanity's cultural development, and seed size increases are taken as one of the earliest domestication traits. Much remains unknown about the ecological drivers and cultural mechanisms surrounding this trait, but morphometric analyses have been crucial to investigate the topic for decades. Measurements on ancient cereal grains show that they evolved to produce larger seeds in their region of origin prior to dispersing beyond their progenitor range. This paper takes a transcontinental (Europe and Asia), long-term approach to comparative morphometric data. Unpublished measurements from over 10 sites of barley, free-threshing wheat, broomcorn millet, and foxtail millet from Central Asia and China have been collected for this study. We have contrasted these with published data from Europe, southwest and Central, East and South Asia. We investigate whether these cereals evolved in parallel or divergent ways across different lineages after they dispersed from their centres of origin; we trace seed size changes from initial cultivation through their spread and eventual adaptation to novel environments. This comparative analysis allows us to discuss rates of evolution and highlight evolutionary trends within some of the most important cereal crops across the Eurasian continent.

This article is part of the theme issue 'Unravelling domestication: multi-disciplinary perspectives on human and non-human relationships in the past, present and future'.

1. Introduction

The domestication of plants and animals allowed for the food surplus that spawned population expansions across the globe—the agricultural demographic transition; these domesticated crops facilitated the formation of denser conglomerations of populations, leading to urbanism and eventually, the formation of social hierarchies and societies segmented into specialized production groups [1,2]. In this way, domestication is the most important phenomenon to allow humanity to culturally develop into modernity, and therefore one of the most pressing areas of study spanning the social and biological sciences. Over the course of the past decade, a paradigm shift has been underway in domestication studies [3,4], as a result, many of the most widely accepted ideas about the cultural mechanisms and ecological drivers pushing this process in prehistory are now under debate again. For the field to move forward, a clearer understanding of the timing and nature of evolutionary trends in these ancient processes is necessary. Morphometric studies are a possible tool through which scholars can contribute to these questions.

Morphometrics is the study of the size and shape of objects and this is widely employed in biology to resolve taxonomic issues and address evolutionary change [5]. In archaeobotany, there has been a recent growth of geometric morphometrics (GMM), with a focus on the statistical characterization of shape as an aid to identification, often characterizing regional and chronological differentiation at an infraspecific level (e.g. [6–10]). The growing emphasis on multi-dimensional shape analyses (GMM) in archaeobotany tends to downplay gross size change. Nonetheless, seed size change is known to be one of the earliest domestication traits to evolve [11–13]. Linear metrical approaches to describing archaeological seed assemblages, i.e. length, breadth (or width) and thickness, have long been used to aid identification and describe variations within ancient grain assemblages. For example, Georg Buschan [14] in an early monograph on archaeobotany and crop evolution compiled measurements of archaeological grains available at the time, mainly from central Europe, to assess temporal trends. Buschan noted that archaeological free-threshing wheat grains of the Neolithic or Bronze Age were on average smaller than those of the Iron Age and later [14]. Later, Jane Renfrew's [15] compilation reflected the state of the evidence in the eastern Mediterranean around the time when flotation sampling became routine archaeobotanical practice, also indicating a trend towards wider grains in later periods. Starting from the 1980s, the use of measurements to set thresholds for distinguishing wild from domesticated plants became more widely employed (e.g. [16–20]). More recently, time series data have been used to quantitatively trace the rate of evolution of plant species and the adaptation of crops to new environments (e.g. [6,13,21–23]). A few recent publications have looked at regional and/or individual species-focused datasets to investigate issues of evolution—e.g. Liu et al. [24] for wheat evolution in East Asia; Fuller et al. [13] for wheat and barley evolution in Europe and the Near East; Motuzaite-Matuzeviciute et al. [25] for barley seed size increase in highland Central Asia, and Ritchey et al. [26] for barley grain size in relation to cuisine preferences in East Asia. Although metrics are widely reported, a macro-regional compilation of trends, as we report here, is novel.

In this paper, we look for broad, temporal trends across crops and between regions through time. We expand upon previous publications about archaeological seed metrics and create a diachronic, transcontinental database of linear measurements of domesticated grains recovered from archaeological sites spanning ten millennia and two continents. Through this database, we highlight the potential of the analytical use of cereal grain measurements. We combine published and unpublished quantitative data on cereal grain size of four Eurasian cereal crops, including barley (Hordeum vulgare) and its naked and hulled varieties; free-threshing wheat (Triticum aestivum, with recognition that some tetraploid free-threshing grains will sometimes be included); broomcorn millet (Panicum miliaceum); and foxtail millet (Setaria italica). These four species featured prominently in the trans-Eurasian exchange, reflecting the establishment of early eastward and westward routes of diffusion and later exchange, linking opposite ends of the Eurasian continent, and contributing to agricultural diversification over the course of the Bronze Age (ca third/second millennia BCE). Scholars have argued that the dispersal of these species contributed to the intensification of local agricultural systems and the development of crop-rotation cycles (i.e. [27–30]).

The data collected for this study are modelled using linear trajectory graphs, visualizing size change over time, and then subdividing by macro-regions (East Asia, Central Asia, South Asia, southwest Asia and Europe). We map out the length and width measurements from archaeobotanical datasets, with an extension of the data using modern or historical landraces, acquired from germplasm facilities and adjusted based on charring experiments, as explained below. Genetic studies have shown that the populations in each macro-region of these four generic-level crop clades remained largely isolated after they dispersed from their centres of origins (e.g. barley: [31,32]; wheat: [33,34]; Panicum: [35]; Setaria: [36]. In this way, we can contrast processes of evolution in grain size that occurred largely independently in each of the macro-regions. These data will depict: (i) the extent to which grain size continued to increase after the crops dispersed from their centres of origin, highlighting that initial domestication was not the only period of important grain size change; (ii) consider how comparable this was across regions; and (iii) explore if parallel evolutionary trends exist across the different crops within the same region.

(a) Factors affecting seed size

Seed sizes are both impacted by genetic programming (evolution) and developmental responses (plasticity), whereas developmental responses fall along a genetically programmed reaction norm and can be affected by human behaviours (e.g. irrigation, manuring and weeding) or environmental variables, such as elevation, precipitation, soil nutrients, soil salinity, solar insulation levels, temperature fluctuations and so on. Each species has its own range of developmental responses [37,38]. Another source of variation may be the recruitment and fixation over time of genetic loci (QTLs, Quantitative Trait Locus) of very minor effect to add to the development of gene variation [39]. Lastly, seed size can be further influenced by archaeological preservation conditions, notably during carbonization [40–45]. Scholars have already argued that seed size resulting from developmental responses are largely averaged out in the archaeological record, as archaeobotanical assemblages are palimpsests of differing seasons, with each annual season representing slightly different temperature and precipitation inputs, and special cultivation, with plants grown at a field edge receiving different irrigation inputs than those at the core [25]. This averaging effect serves to reduce the impacts of developmental plasticity on linear metric data, leaving a mean line that more closely follows genetically programmed mean size, with the ends or the reaction norms further removed as additional specimens are added to the metadata. Changes in the range of variation at a given time slice can either represent a greater diversity of local ecotypes or a higher diversity of growing conditions and ecological pressures.

Research has shown that cereal grains underwent substantial seed size increase during the first phases of domestication of at least a 20% increase in average breadth or thickness (representing a larger increase in volume or mass), but more typically 60% (20%–60%), and in some species up to 140% or more [6,22,46,47]. Kluyver et al. [48] found that the seeds of domesticated vegetable crops, which are not cultivated for their grains, have seeds that are from 20% to 170% larger than their wild progenitors. The realization that all domesticated plants, whether cultivated for their seed or vegetative parts, increase in seed size during the initial evolution of domestication traits, challenges arguments for intentional selection for larger seeds. Greater seed size can be regarded as part of a wide suite of traits that made cultivated plants ‘proficient competitors in resource abundant environments’ [49, p. 5]. This raises the possibility that some of these changes are pleiotropic, with genes affecting more than one size trait. However, it is also clear that seed size is impacted by multiple genes with varied quantitative effects [12,50–52].

Scholars have heavily debated over the ecological factors that drove this seed size increase, with increasingly more domestication researchers pushing models that focus on unconscious processes [53,54]. A clearer understanding of the rates of seed size increase and ecological constraints affecting those rates should help sort through the proposed drivers. Among the unconscious models of domestication, many scholars have theorized mechanisms, such as competition (often sibling–sibling competition in fields composed of a single crop—competition theory), in which competition between seedlings favours those that more rapidly establish root systems and above-ground photosynthetic area ([12,23,39,49] see also [11,55]). The competitive selection framework for understanding how large grain size evolves under conditions of enhanced seedling competition can be taken to predict that gene loci (QTLs) of large effect will most likely get selected for and fixed early (during initial domestication), given that plants with them have a more substantial competitive advantage under conditions of early cultivation [39,47]. Thus, some regional size change patterns may represent additional alleles adding effects on seed size under the continuing pressures of cultivation from which seed size change began. Since QTLs are not exchanged between species, any parallels across taxa must imply shared environmental selection. Other scholars have argued that larger seeds may have an advantage when the seed is sown at greater depth owing either to intentional burial or tillage [54,56,57], but some experimental studies have suggested that this is not always the case [58]. Other scholars have favoured ecological-release arguments, claiming that increased resource availability—water and nutrient input, reduced herbivory and parasitic pressures and reduction in inter-species competition all allowed plants to invest greater nutrient stores in their offspring [59]. A defining feature of ecological release is niche shifts, which may be accompanied by either an increase in morphological variation or a shift in the mean morphological values in a population [60]. Ecologists have noted that early domestication traits seem to all be acquisitive, in that plants may have evolved to maximize growth and reproductive success, at the expense of traits associated with defence and ecological adaptation (i.e. [61,62]). Spengler has suggested that seed size increase might also have been tied to a loosening of the seed-dispersal constraints—essentially, that plants were freed from the limitations on seed size imposed by the effectiveness of their progenitor dispersal mechanism [63]. Not all these drivers are mutually exclusive, and they may have compounded selective forces to drive evolution of acquisitive traits, such as greater seed provision, allowing increased competitive advantage for plants under cultivation in contexts of increased intraspecific population density and competition.

Seed size changes after crops spread outside their centre of origins can be regarded as selection towards regional varieties, as suggested by variation and fluctuation across regions of Europe documented in barley, emmer and einkorn wheat [13]. We assume that any visible diachronic change in seed size in the archaeobotanical record over the centuries represents evolutionary processes rather than phenotypic variation, which would fluctuate seasonally and across local landscape over shorter time scales [13,40]. As the archaeobotanical record is composed of seeds spanning many seasons and a range of microenvironments, the diversity of developmental forms would be averaged or appear as a range (see discussion in [26]).

2. Material and methods

Linear measurements of length, width and thickness on barley (H. vulgare), including hulled (H. vulgare var. vulgare) and naked barley (H. vulgare var. nudum), free-threshing wheat (T. aestivum sensu lato), and broomcorn (P. miliaceum) and foxtail millet (S. italica) grains have been gathered from the archaeobotanical literature, the authors' own archaeobotanical collections and unpublished material (Fuller D.Q, 2023; Mir Makhamad B, 2023; Dal Martello R, 2023; see the electronic supplementary material, S1). This follows the method of previous studies that have used similar data compilations to track grain size changes in relation to domestication (e.g. [13,22,64]). In some cases, when measurements were not reported, but scaled photos of the grains were published, dimensions were obtained from the photographs. This was undertaken with the use of open access software ImageJ (65; https://imagej.net/ij/download.html); the scale was set based on the one provided in the published photo, and measurements acquired. The nature of the data is indicated in the Notes column of the electronic supplementary material, S1, available online. In addition to archaeological measurements, modern grain size was obtained from reference material from the Archaeobotanical Reference Collection at the Institute of Archaeology, University College London, and from the US Department of Agriculture Germplasm Resources Information Network. This set of modern measurements for each species and macro-region has been included to account for the modern observable stage of evolution; this modern comparison was used only in the macro-region of provenance. Since charring leads to shrinkage, and charring experiments on cereals have estimated that typically there is a 10–20% reduction of seed size post-charring (e.g. [22,40,42,66–72]), we have applied a −10% correction factor to modern measurements so to make them comparable to archaeologically charred material. This is the correction factor applied by previous similar studies (e.g. [13,22,64]). Past morphometric studies on cereal grains assumed that all archaeological seeds underwent a similar rate of shrinkage, and the possible error range is uniform across the data or averaged out in a similar way to the plasticity ranges mentioned above (e.g. [13,21,40]); therefore, we did not apply any correction factor to the archaeological material. While charring experiments indicate that uniform shrinkage is not strictly true, unaccounted for variability is expected to add some noise to the dataset, but which should be within the distribution of data accounted for with the standard deviation (s.d.) estimates. We followed methodology previously successfully applied on studies on other species (i.e. emmer) outlined in Fuller et al. [13]; other studies also include [22,64].

The compiled data were divided into six macro regions, countries grouping is outlined in the electronic supplementary material, S2 (see also figure S1 for a map showing location of sites and figure S2 for cumulative counts of the compiled sites for this study, illustrating regional and chronological gaps in the data). Seed size measurements compiled for this study come from 485 archaeological sites (see table 1; electronic supplementary material, S2, figure S1), including 10 unpublished sites, spanning from the ninth/eighth millennium BCE to the present day. Although elevation data were also collected for each data point (see the electronic supplementary material, S1); however, since elevation is not an independent variable, but it is constrained by the geographical location of the sites, we postulate that this is accounted for by looking at each region separately.

Table 1. Summary of number of archaeological sites with reported seed measurements compiled for this study, shown per macro-region and species, including indication of reported number of seeds measured when available[a]. (Chronological information on the dataset is provided in the electronic supplementary material, S2 and figure S2.)

species	southwest Asia	southern Europe	northern Europe	Central Asia	South Asia	East Asia	total sites	seeds measured
Hordeum vulgare	10	35	45	9	3	27	129	7580
H. vulgare (hulled)	16	14	26	5	6	25	92	5399
H. vulgare (naked)	6	26	51	9	1	59	152	9475
Triticum aestivum	38	41	45	20	10	10	164	10 843
Panicum miliaceum	6	15	34	15	1	53	124	3699
Setaria italica	3	4	3	11	4	35	56	2078
totals	79	135	510	69	25	209	(717)[b]	36 074

[a] Many reports do not state the number of seeds measured, therefore, the total number of seeds measured indicated here is lower than the overall total number of seeds measured.

[b] Since several sites have multiple species in their assemblage, the total number of sites is lower than the number shown in the summary table, where it was not possible to avoid duplicate counts. Individual site count totals to 485 as indicated in text

Although seed size is widely reported in archaeobotanical literature, there is not a standardized system to report these metrics and different authors working in different regions report metrics differently. Some publications report averages, or means, some list minimum and maximum size, others include a list of individual grain measurements. We gathered all available measurements, and when minimum and maximum size were provided with a sample size of the population measured, we calculated averages and s.d. through a standard formula that assumes a normally distributed population ([73], table 27), by the formula

$$\mathrm{s.\,d.} = \frac{L^{\max} - L^{\min}}{f^{n}},$$

where Lmax and Lmin are the largest and smallest measurements, and fn is the factor taken from the above table based on sample size. This approach was ultimately derived from the calculations of Tippett [74], based on the range between extreme individuals. Tippett's tests also indicate that even in non-normal and skewed distributions, the results are not significantly different. Previous studies of cereal grains showed that width is the most affected dimension displaying the greatest changes through domestication [12,21]; in our analysis, however, we examined both width and length to check whether width continues to be the main affected dimension and to assess the change in overall seed size (figures 1–4).

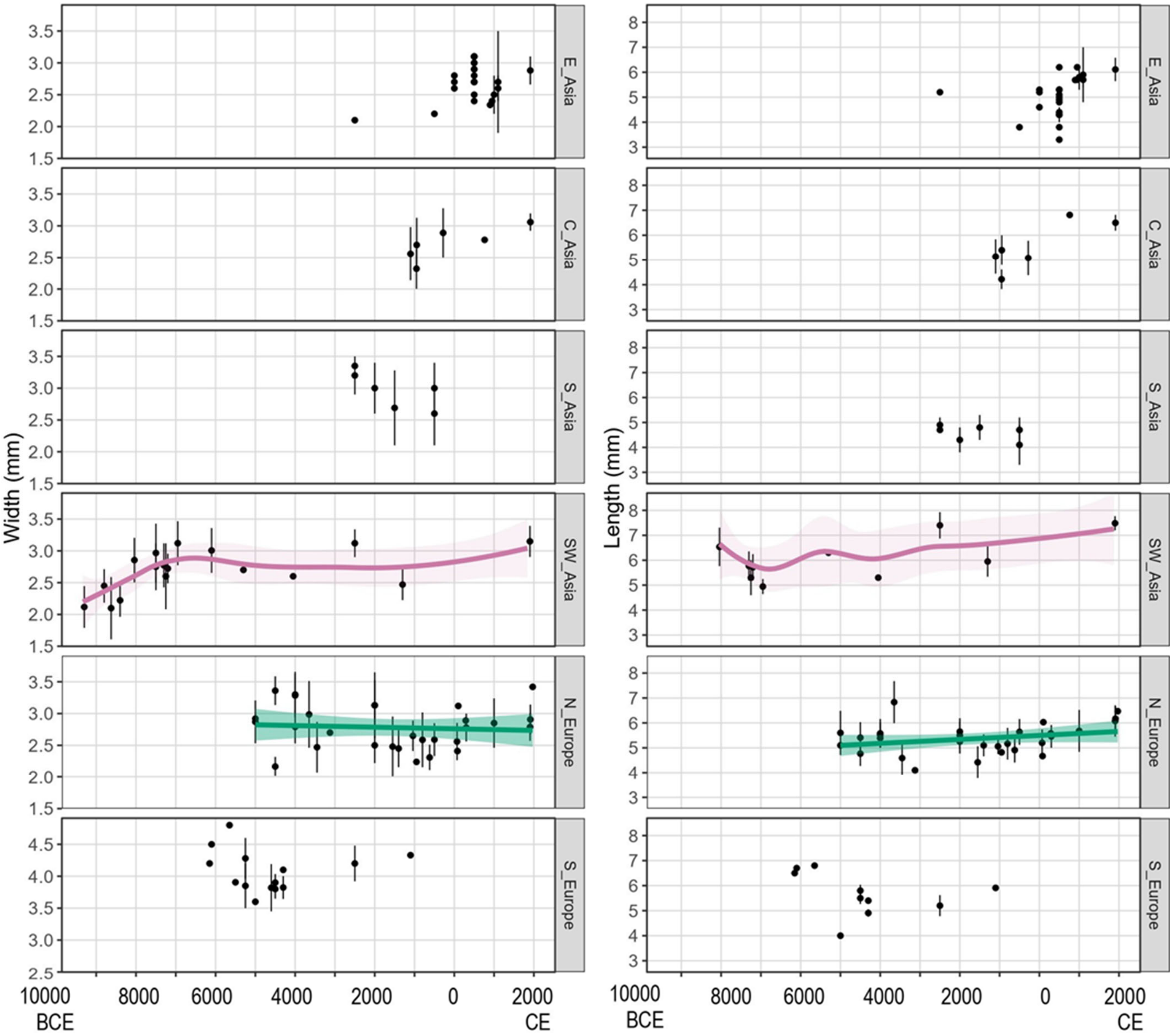

Figure 1. Locally weighted scatterplot smoothing (LOESS) trends of hulled barley grain size from all macro-regions of study. The coloured shade indicates the confidence interval for each region. Sample size (number of sites) n = 98; East Asia = 26; Central Asia = 6; South Asia = 6; southwest Asia = 17; northern Europe = 29; southern Europe = 14 (see the electronic supplementary material, S1). Made with ggplot2.

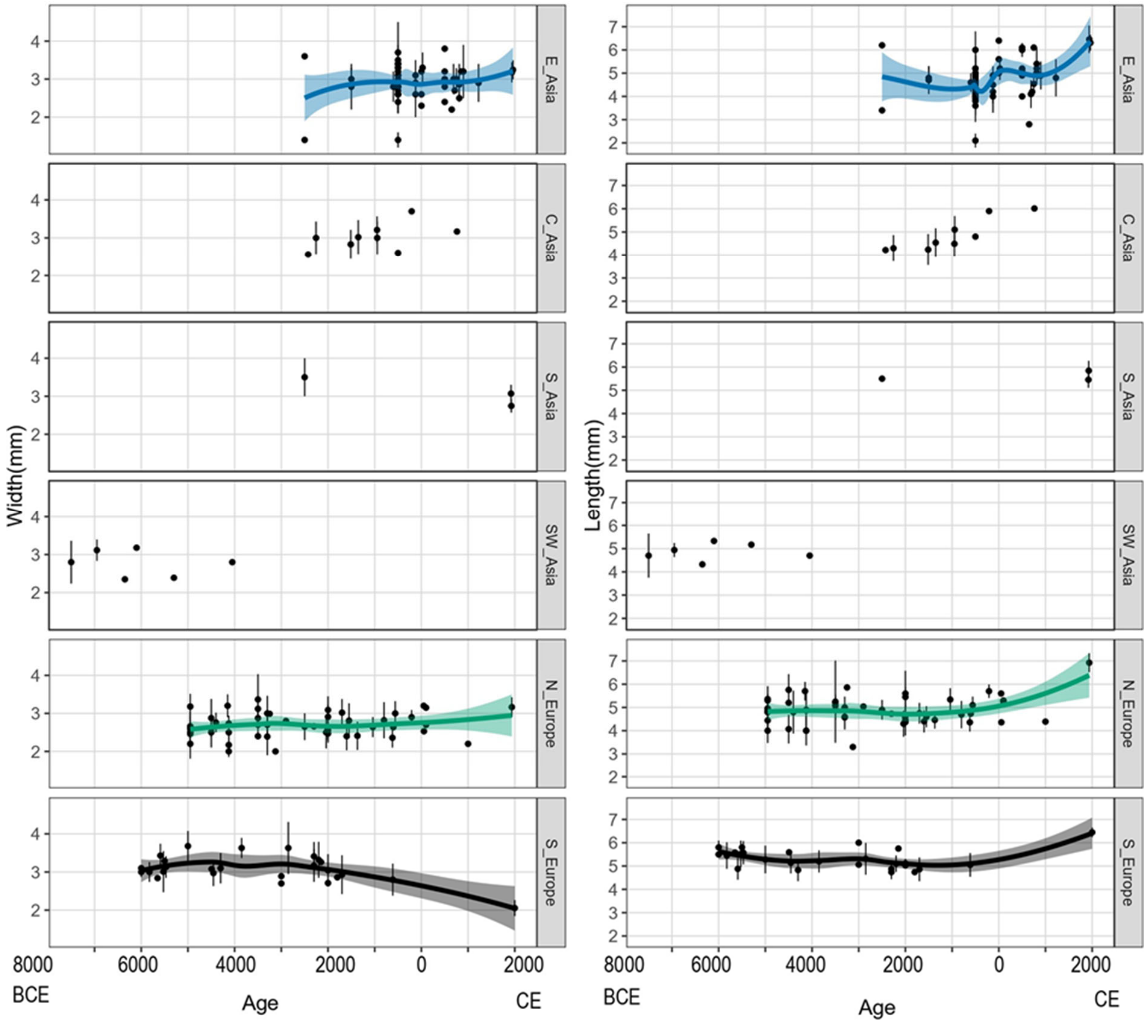

Figure 2. LOESS trends of naked barley grain size (width on the left and length on the right) from each macro-region. The coloured shade indicates the confidence interval for each region. Sample size (number of sites) n = 158; East Asia = 61; Central Asia = 9; South Asia = 3; southwest Asia = 6; northern Europe = 52; southern Europe = 27 (see the electronic supplementary material, S1). Made with ggplot2.

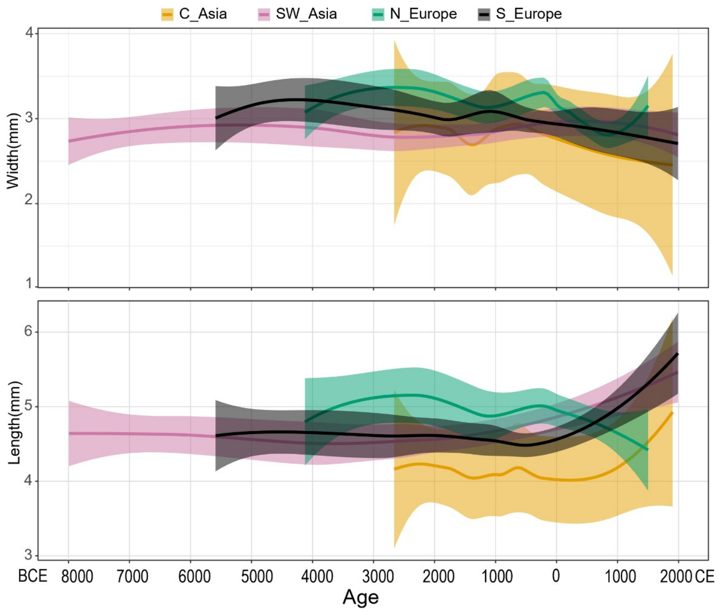

Figure 3. Overlapping LOESS trends of free-threshing wheat grain size. The coloured shade indicates the confidence interval for each region. Made with ggplot2. See the electronic supplementary material, S2, figure S7 for separated regional trends.

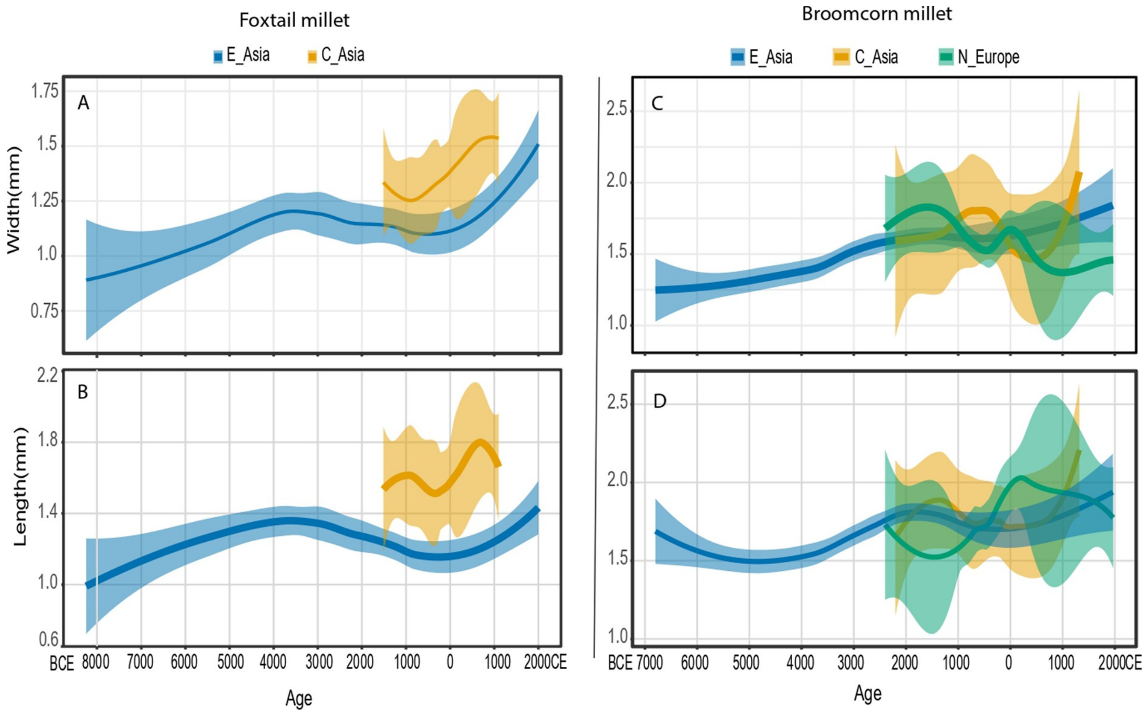

Figure 4. Overlapping LOESS trends of broomcorn millet (right) and foxtail millet (left) grain size. The coloured shade indicates the confidence interval for each region. Made with ggplot2. See the electronic supplementary material, S2, figure S7 for separated regional trends.

All statistical analyses were performed in R, version 4.3.2 [75] using the R-Studio interface. All figures in the text were made using ‘ggplot2’ [76]. We plotted the averages and s.d. for all length and width measurements against the median age of the assemblages, which was obtained from the established chronological occupation of each site as reported in the available literature (electronic supplementary material, S1). We did not include barley grains measuring less than 2 mm in length, and broomcorn millet grains measuring less than 1.25 mm, as these are representative of either wild or immature grains; we also excluded hulled barley grains measuring greater than 9 mm in length as these are indicative of unprocessed grains (grains that were not dehusked). Finally, we excluded measurements based on a single grain from any given time period, as these individual data points may not be representative enough for statistical analysis. To assess grain width and length changes over time, we applied a locally weighted scatterplot smoothing (LOESS) method to each region. This is one of the non-parametric regression techniques, and it is a more flexible tool to smooth data and better handle complex, noisy and irregular sample data ([77]; figure 1; figure 2; electronic supplementary material, S2, figures S3 and S7–S9). The solid line in the graphs represents the LOESS trend, while the shaded area indicates the confidence interval; a thick shaded area suggests low confidence, and a narrow shaded area suggests high confidence. However, LOESS trendlines for regions with insufficient data (n = 20) were not shown, as they cannot reliably demonstrate trends. For each crop, we also plotted regions with apparent trends simultaneously (figure 3; figure 4; electronic supplementary material, S2, figures S4–S6). To ensure clarity in the overlapping trends figures, individual data points were omitted to better highlight the trends. Given our dataset is based on average values of each site, we decided against using the Mann-Kendall test to test the robustness of the trend owing to several issues: (i) averaging data smooths out crucial variations and extremes, reducing the test's ability to detect significant trends; (ii) it also introduces serial correlation, violating the test's assumption of independent data points; and (iii) fewer data points owing to averaging decrease the statistical power of the test, limiting the reliability of trend analysis.

Given the extensive amount of literature consulted and the large numbers of different authors measuring the grains, some imprecision and errors are inevitable; however, we assume that when adopting such a large-scale and long-term perspective, the extent of error is smaller than the visible chronological patterns of change.

3. Results

(a) Barley

Cultivated barley (H. vulgare) evolved from the wild H. vulgare ssp. spontaneum in southwest Asia around the eighth/seventh millennium BCE, with a polycentric origin and genetic contribution from several wild barley populations, including from Mesopotamia, northern and southern Levant, Syria, and Central Asia [78–80]. Wild barley has hulled grains, but some domesticated varieties show naked grains, where the paleas covering the grains are more easily disarticulated or readily removed after threshing. Ancient naked grains have been reported for example from Hacilar (ca 6200−5800 BCE) and Ali Kosh (ca 6400 BCE [81,82]). Generally speaking, (hulled) barley grains show a marked increase in width and thickness, but not length, as attested at sites in southwest Asia, including at Jerf el-Ahmar and ZAD-2 [12,13,18,20,40,83]. For hulled barley, this initial increase in grain size can be attributed to the first phase of domestication, which served to increase the volume of the starchy endosperm to a greater degree than increases in length would. For southwest Asia, the initial increase in width contrasts with an apparent decrease in length in the later Neolithic (after the ca 7500 BCE; figure 1). From the sixth millennium BCE onwards, the earlier increasing trend in width transitioned towards a more stable form. By contrast, the initial earlier decreasing trend observed in length started to increase from the Bronze Age onwards (fourth millennium BCE). Outside its region of origin, hulled barley shows several differing regional patterns. First, there is a decrease in width but an increase in length in northern Europe (figure 1). Second, there is an apparent increase in length in Central and East Asia and southern Europe, especially over the past 3000 years (figure 1). The data presented by Ritchey et al. [26] also indicated an increase in barley size after 1000 BCE for China; although, hulled barley only spreads into East Asia about two millennia ago. The lack of trendlines in these regions may be owing to relatively small sample sizes (e.g. Central Asia and South Asia) or skewed data distributions (e.g. East Asia with a low confidence level). Individual metric data for each region are needed for these regions to draw definitive conclusions.

Except for southwest and South Asia, naked barley grain length shows a significant increasing trend for all other regions (figure 2). The lack of trends from South and southwest Asia may be owing to the extremely low number of points (only one ancient datapoint for South Asia, and six for southwest Asia). In northern Europe and East Asia, both grain width and length increased, in conjunction with the adoption of this species as a staple crop in these regions (figure 2). In southern Europe, naked barley grains show a decrease in width and an increase in length through time (figure 2). However, these trends may be skewed by the most recent data points and a large gap in data from 700 BCE to today. If these trends are confirmed by more data points for the last 2700 years in future research, this could indicate a trend towards longer, skinnier naked barley in southern Europe diverging from generally larger barley grains in northern Europe and East Asia (figure 2).

(b) Free-threshing wheat

Free-threshing bread wheat (T. aestivum) is a hexaploid wheat species that evolved through hybridization between already domesticated tetraploid wheat and the goat’s-face grass Aegilops tauschii Coiss. sensu lato (A. tauschii ssp. strangulata according to some recent studies, e.g. [34,84]). Phyologenetic data suggest at least two parallel origins of hexaploidy in wheat from different tetraploid Triticum turgidum genetic backgrounds [85,86]. Archaeobotanical finds of T. aestivum have been found in northern Levant, from sites along the upper Euphrates from southern Turkey (e.g. Cafer Höyük IV, ca 7350 BCE), and Syria (Abu Hureyra 2, ca 7000 BCE; El Kowm II, ca 6700 BCE) [87], and eastwards in central Anatolia (e.g. Asikli Höyük aceramic Catalhöyük, ca 7000 BCE [88]. There currently are no early finds close to the Caspian Sea where the most closely related Aegilops populations occur.

Wheat grain size shows an increase early on at sites located in southwest Asia [20,40,83], the area of origin for this species (figure 3). However, when considering the long-term data, the overall width and length remained relatively stable over the last 10 000 years. In southern Europe, where this species spreads around the fifth millennium BCE, there is an overall slight decreasing trend for width, but no change in length except for the modern data. In northern Europe, free-threshing wheat spreads around the fourth millennium BCE. After an initial increase, both width and length decreased over time. In East and South Asia, no apparent trends have been detected, most likely owing to the limited sample size (electronic supplementary material, S2, figure S7). In Central Asia, although a LOESS analysis has identified a trend for both width and length, the confidence interval is relatively wide. This may be owing to substantial variations in individual data points that deviate from the mean, potentially explaining the absence of significant trends in these regions (figure 3).

(c) Millets

(i) Broomcorn millet

Broomcorn millet was most likely domesticated in northern or western China around the sixth millennium BCE [23,89]. Most of our data for broomcorn millet derives from East and Central Asia, and northern Europe (table 1; see also the electronic supplementary material, S2, figure S2). In East Asia, broomcorn millet grains show a significant steady increase in both width and length over time (figure 4, right). A very weak increase in width and length is seen in southwest Asia; however, the limited sample size for this region could not produce a LOESS trend (electronic supplementary material, S2, figure S8). The datapoints for Europe show a wide range of sizes, preventing the production of LOESS trends and making changes in these regions less clear (electronic supplementary material, S2, figure S8).

(ii) Foxtail millet

Foxtail millet evolved from the wild Setaria viridis populations of northern China [90,91]. It was also most likely domesticated between the eighth and sixth millennia BCE, based on evidence for shape and size change in grains [92]. This species, although being a staple crop within the early Chinese states, did not spread or get adopted as much in other regions, where, instead, broomcorn millet was adopted more readily and became prevalent, thanks to its ability to adapt to a wider range of climatic and growing conditions. For this reason, metrics of foxtail millet grains are available almost exclusively from East and Central Asia (table 1; electronic supplementary material, S2, figure S9). In East Asia, grains show a continuous increase in both width and length over time (figure 4). In Central Asia, the width increased over time, although there are large variations in width from 1000 BCE to 500 CE. By contrast, the length remained relatively stable with less variation during the same period (figure 4, left). Owing to the limited sample size, more data are needed to confirm these trends. Furthermore, from 2000 BCE to 1000 CE, both dimensions of the grains were generally larger in Central Asia than in East Asia.

4. Discussion

Archaeological grain size measurements (traditional metrics) are useful for finding temporal and geographical trends, but these are not without their limitations. Only through large compilations of such data are larger-scale patterns recognizable, which in turn raise new questions about the evolutionary processes underlying grain size and shape in post-domestication time periods. This study has identified regional patterns in grain size change that differ between regions of Eurasia but show parallels across species. Nevertheless, the limitations of current data must be kept in mind. The size of samples is not equivalent across taxa and across regions. There is far more data available from Europe and East Asia than from

South Asia, and generally larger datasets for wheat and barley as opposed to millets. Part of this is the result of certain laboratory traditions in selected countries being more prone to measure and report measurements. There may be some variations in precisions based on how measurements have been made, but it is unlikely that patterns we have identified result from such biases, as these would be expected to correlate with laboratories rather than with period or region. In addition, as most data are reported only as mean, maximum, minimum and sample size, our analyses rely on the assumption of a normal distribution which would not be met if a given site has multimodal data that would be expected if multiple varieties or landraces were grown alongside each and contributed to a site assemblage. Only by reporting and then analysing seed-by-seed measurements can within-site variability be better assessed. The impact of charring on grain metrics also adds noise as the amount of shrinkage may vary between charring conditions in the past, which we have no way to control for, and may differentially affect length and breadth to some degree. Nevertheless, such concerns are expected to only add a bit of noise to what appear strong macro-regional and temporal trends, which should encourage more effort to report measurements on archaeological grains.

(a) Regional variations in the patterns

Across all species considered, changes in width are more clearly visible earlier on, associated with the divergence of each species from their wild ancestors. This matches previous observations that domestication was associated with an increase in grain volume mainly through increasing girth (width and thickness), which has been demonstrated across cereals that have long time series size data associated with early cultivation and domestication [12,22,93–95]. These studies illustrated that there was a relatively rapid (over the course of two millennia or less) increase in grain width, resulting in greater endosperm mass or volume, at the onset of cultivation or slightly thereafter [13,22,39]. These observations illustrate that geographical isolation from the progenitor population was not essential for domestication, as crops do not show increasing size trends after dispersing out of the range of wild progenitors (nor do crops continually grown within the progenitor ranges continue to increase in grain size). The phase of plateaued size change was interrupted by later trends of size change, which could vary in extent and direction between regions, and only in recent centuries additional changes were brought about by directed breeding in modern crop varieties. This observation holds strong bearing on interpretations of the evolutionary drivers, as it shows that: (i) crops evolved the earliest traits of domestication within the ranges of their wild progenitors; (ii) the evolutionary pressures either reached an equilibrium between grain size and selection (i.e. biological and ecological forces constrained further size increase) or the pressures abated after the first few millennia of growing; and (iii) despite most grains showing a general trend towards increased mass after the industrial era, from the early domestication phase until this point, there is an extended period of regional divergence, either driven by stochastic forces or varying ecological stressors. Since convergent phenotypic similarity between unrelated taxa shows that different genetic backgrounds can result in similar adaptive solutions when subjected to similar pressure, this is seen as strong evidence for convergent or parallel evolution [96–98]. Spengler [59] compared evolution under domestication to that of plants on islands, which often show seed size increases, probably owing to ecological release. It is conceivable that some varieties evolved initially in isolated habitats (i.e. small agricultural fields). In one documented case, translocation to the island of Cyprus during the domestication process, led to a speeding up of the increase in grain width in einkorn wheat [94]. Nevertheless, the specific trends that we identify here took place over broad regions, suggesting sustained and widespread selective pressures also operated in large mainland regions.

While the parallel trends in wheat and barley in Central and East Asia have received substantial attention in recent years (i.e. [24–26,99]), the data analysed in this article indicate parallel trends in other regions such as northern and southern Europe, as well as parallel trends in millets. Overall, the data confirm a directional increase in grain breadth across all species during early phases of cultivation and domestication, followed by differentiation between regions and different directional trends. This diversification in trends of size evolution is indicative of the evolution of different regional varieties or preferences. The regional similarity across species indicates that a similar set of selection pressures acted with similar results across different species.

In East Asia, barley shows long-term evolution towards larger-seeded varieties. Even if there was some initial preference for smaller, compact wheat and barley (see below), they ultimately became bigger. Millets in East Asia also show trends towards larger seeds. Similar trends are seen in Central Asia and northern Europe while opposite trends were typical in southern Europe.

Within Europe, there appear to be mostly opposing patterns in southern Europe when compared to northern Europe. In the southern region, grains regardless of the species show a general decrease in width over time, which is especially visible for naked barley and wheat. By contrast, they tend to get longer and bigger in northern Europe. It is unclear what to attribute this divergence to. Higher rainfall in the north would mean that cereals in northern Europe tended to be better watered. There was also a change in typical seasonality, with summer cropping and photoperiod neutral varieties more typical in the north, which might contribute to different grain sizes.

Metrics from South Asia are the least numerous compared to the other macro-regions and this limits our ability to make any meaningful interpretation. The only visible characteristic is that of wheat grains becoming wider and shorter through time. This is in line with the evolution of compact-seeded wheat varieties in this region, including compact and dwarf wheats (see below).

(b) Explaining compact grain size

Several arguments have been proposed for the increases in cereal grain breadth attested after the initial phases of cultivation and domestication, such as better watering through irrigation [29,100]. However, in parts of Asia, a trend towards decreases in length, leading to more spheroidal grains, also occurred. Some scholars have inversely linked this trait change to adaptations to aridity and water stress [100,101]. Sphaerococcoid wheat (Triticum aestivum ssp. sphaerococcum) is thought to have evolved in ancient Pakistan and has been hypothesized to have been a genetically underpinned example of such an adaptation, a trade-off as productivity of sphaerococcum is lower [102]. Short-grained wheat, however, is also known for extremely high elevations in medieval Nepal (103) and the semi-dwarfing traits (the Rht genes) for Green Revolution wheats were obtained from Japanese landraces [104]. Spengler [105] suggested that the driver for the evolution of highly compact forms is likely to parallel the reasons why Borlaug selected these crops for the Green Revolution breeds. Interestingly, his reasoning had nothing to do with grain size, but rather allometric changes in overall plant height, which reduced lodging. Both the Rht semi-dwarfing Japanese wheat and the Indian dwarf wheat (the sphaerococcoid syndrome) express a pleiotropic link between plant squatness and inflorescence compactness, resulting in seed compactness. Sharp shifts in water availability (high water inputs in the spring and arid conditions in the summer—or reversed for winter wheat) and high winds can cause plants to fall over or lodge, resulting in grain losses. It is likely that the dwarfing forms were simply the descendants of the crops that remained standing in a field after the remainder of the plants lodged over. Indian dwarf wheat also expresses greater tillering, and a syndrome of linked traits. This theory suggests that grain size was not even the trait of selection and that the evolutionary shift probably occurred over millennia without humans perceiving it. The genetic mechanisms behind the various semi-dwarfing wheat forms are different, suggesting selective pressures repeatedly driving the domestication of these lower-yielding crop morphs.

An alternative explanation has been proposed by Liu et al. [24,26,106], who suggest that compact size of both wheat and barley as attested in Bronze Age China were actively selected for culinary preferences in the region. This refers to the comparison of data from the Inner Asian Mountain Corridor region through Hexi, into monsoonal China. This would imply conscious selection by farmers favouring smaller grains more suited to being boiled or steamed [26]. In East Asia, the shortening of grains in both wheat and barley during the Bronze Age suggests similar conditions of selection, even though wheat and barley are often not co-distributed on the same sites in Early Bronze Age China. However, as noted above, compact grain forms are not universally found in China but tended to be more typical of earlier (Early Bronze Age) examples from the central plains. As boiling and steaming persisted across East Asia, the trend towards increasing grain sizes over the last 3000 years seems to suggest that other pressures drove the crop evolutionary trends. For the higher elevations of the Tibetan plateau, outside the boiling zone, it was suggested that larger and longer grains better suit a flour-based cuisine [26]. Although, the opposite trend is noted in the Mediterranean where flour-based cuisine was well-established, indicating that a simple explanatory framework that links conscious choice in grain size to the use of boiled flour-based cuisine falls short.

5. Conclusions and future directions

As demonstrated in this study, seed size is a useful measure of change to track the evolution of cereal grains through continuous human use over millennia. Morphometric studies on cereals have demonstrated a substantial, initial seed size increase, linked with the differentiation of the cereals from their wild progenitors. Our study has shown that the extent of change in grain size in that initial increase was generally larger than any changes since, including modern breeding. After two or three millennia or more, the rate of size increase appears to plateau. During this extended period, local differences across macro-regions are visible, for example following their spread to Europe, the seeds of the cereals studied in this paper appear to overall shrink in size before increasing again only in the last one to three millennia. In Central Asia, instead, there is a trend of continuous increase for all species studied. This is paralleled by grain increases in China starting about 3000 years ago.

The competing hypotheses for selection pressures driving these trends include unconscious selection and environmental adaptations or some conscious selection in relation to cultural preferences, such as how they relate to processing and cooking traditions. The long timescale in many of these regional trends would involve dozens to even hundreds of human generations. This argues against arguments based on intentional breeding in prehistory, such as the recent claim that East Asian grains were specifically bred for culinary preferences. The fact that most historical landraces and modern varieties of these crops, produced over the past couple of centuries with modern cultivation practises and breeding programmes, are on average larger than ancient forms suggests that these crops did not stop increasing in size owing to a biologically determined absolute constraint on size. The archaeobotanical evidence for grain size offers a robust line evidence for evolutionary processes but has gaps to be filled in future research.

Ethics

This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility

All data presented are available online as the electronic supplementary material [107].

Declaration of AI use

We have not used AI-assisted technologies in creating this article.

Authors' contributions

R.D.M.: conceptualization, data curation, formal analysis, methodology, visualization, writing—original draft; Y.V.W.: software, visualization, writing—review and editing; B.M.M.: data curation, writing—review and editing; R.N.S.: conceptualization, formal analysis, funding acquisition, supervision, writing—review and editing; D.Q.F.: conceptualization, data curation, formal analysis, methodology, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration

We declare we have no competing interests.

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Footnotes

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