Veget Hist Archaeobot (2012) 21:131–145
DOI 10.1007/s00334-011-0329-8

ORIGINAL ARTICLE

Cultivation as slow evolutionary entanglement: comparative data on rate and sequence of domestication

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Received: 13 May 2011 / Accepted: 10 October 2011 / Published online: 1 November 2011

Abstract Recent studies have suggested that domestication was a slower evolutionary process than was previously thought. We address this issue by quantifying rates of phenotypic change in crops undergoing domestication, including five crops from the Near East (*Triticum monococcum*, *T. dicoccum*, *Hordeum vulgare*, *Pisum sativum*, *Lens culinaris*) and six crops from other regions (*Oryza sativa*, *Pennisetum glaucum*, *Vigna radiata*, *Cucumis melo*, *Helianthus annus*, *Iva annua*). We calculate rates using the metrics of darwin units and haldane units, which have been used in evolutionary biology, and apply this to data on non-shattering cereal spikelets and seed size. Rates are calculated by considering data over a 4,000-year period from archaeological sites in the region of origin, although we discuss the likelihood that a shorter period of domestication (1,000–2,000) years may be more appropriate for some crops, such as pulses. We report broadly comparable rates of change across all the crops and traits considered, and find that these are close to the averages and median values reported in various evolutionary biological studies. Nevertheless, there is still variation in rates between domesticates, such as melon seeds increasing at twice the rate of cereals, and between traits, such as non-shattering evolving faster than grain size. Such comparisons underline the utility of a quantitative approach to domestication rates, and the need to develop larger datasets for comparisons between crops and across regions.

Keywords Domestication syndrome · Unconscious selection · Southwest Asia · Neolithic · Palaeoethnobotany

Introduction

The study of agricultural origins more often than not focuses on plant domestication in the ‘Fertile Crescent’ region of the Near East, which is generally regarded as having the best archaeological record for agricultural origins and also was the source of the main agricultural traditions and crops of European prehistory and later civilizations of the Middle East and Europe. Since the influential work of Childe (1935) in the early 20th century this region has been the primary example of the “Neolithic Revolution.” In this paper we reconsider the uniqueness of the plant domestication in the Near East from a comparative perspective. Did the domestication process and the rate at which domesticated crops evolved in Southwest Asia differ by comparison to crops domesticated elsewhere in the world, i.e., in China, Africa or America? Do agricultural origins represent a special kind of evolution, i.e. is plant domestication qualitatively or quantitatively different from evolution in natural contexts that

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Communicated by F. Bittmann.

Electronic supplementary material The online version of this article (doi:10.1007/s00334-011-0329-8) contains supplementary material, which is available to authorized users.

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did not involve human actors? We examine these issues by calculating archaeologically-derived estimates of the rates of phenotypic evolution during domestication for Near Eastern crops (barley, einkorn, emmer, pea, lentil) and compare them to (a) crops from other world regions (Indian mungbean, African pearl millet, Chinese rice, melon, American sunflower and sumpweed) and (b) to documented cases of microevolution and the fossil record in general. While we conclude that plant domestication in essence does not differ in rates of change or strength of selection from evolution recorded in wild species, we do discover variation between the evolution of different crop groups, e.g. pulses and cereals, and between different domestication traits, especially non-shattering habit and grain size. Finally, we address the question of what accounts for the similarities and variation we find across different instances of domestication. This raises questions about the role of different human behaviours involved in cultivation, in selecting for evolutionary changes in early crops (Fuller et al. 2010a). We suggest that understanding the evolutionary process in terms of geographical mosaics of co-evolution may be useful, while archaeologically we need to take better account of the social organization of the labour invested in cultivation, harvesting and crop-processing.

Plant domestication has often been regarded as a rapid process, due to strong directional selection pressures by human action. Perhaps the best known statement of this kind in Near Eastern archaeobotany comes from the work of Hillman and Davies (1990, 1992) who carried out experimental cultivation and harvesting of wild einkorn in the 1980s. This short gestation model has been a dominant paradigm in textbooks (e.g. Harlan 1995; Bellwood 2005). The assumption that domestication should have occurred rapidly, and by inference was the product of strong artificial selection pressures, underlies many genetic models of domestication either explicitly (e.g. Zohary 2004; Innan and Kim 2004; Zhang et al. 2009) or implicitly (e.g. Heun et al. 1997; Badr et al. 2000). The short gestation model continues to have its proponents (e.g. Honne and Heun 2009; Abbo et al. 2010a; Haldorsen et al. 2011; Peleg et al. 2011) although archaeobotanical evidence that fits it has not been forthcoming.

The short gestation model has been tacitly accepted in part because it is logical and in part because archaeobotanical evidence from which to directly assess it has been very limited. As reviewed in Fuller (2008) there has been a slow, but steady increase in the number of Neolithic sites of the Near East subjected to systematic flotation, archaeobotanical analysis and full publication, such that published assemblages from flotation reached about 40 by the year 2000. However, hard evidence of the key domestication indicator, non-shattering rachises, has been slower to accumulate. The first quantified data on non-shattering was the barley rachises examined by Van Zeist in the early 1980s from Aswad and Ramad (Van Zeist and Bakker-Heeres 1985). Improved methods for distinguishing variation in the rachis remains of barley and the spikelet forks of emmer have been published in recent years, including work by Kislev (1997), Colledge (2001) and Tanno and Willcox (2006). It is only in the last decade that substantial datasets (numbering a few thousand rachises for each of einkorn and barley) have been published (Fig. 1 in Allaby et al. 2010). Tanno and Willcox (2006) compiled a chronological series of data from 6 sites in the Near East to look at the changing proportion of wild to domesticated cereal morphotypes and came to the conclusion that domestication was a slow process, on the order of 3,000 years. While their data combined einkorn wheat and barley into one series, Fuller (2007) separated einkorn and barley with a larger dataset (22 sites) and compared the two species, concluding that non-shattering indeed evolved slowly. When estimated from the first appearance of a minority of non-shattering types, non-shattering in wheat may have evolved slightly faster (~1,500 years) than barley (~2,000 years). A larger dataset, with improved identification criteria for wheat spikelet fork domestication status, is reported in this volume by Tanno and Willcox (2011). Although this has not been incorporated into the analyses reported here, it would appear to confirm the same pattern. Equivalent archaeobotanical evidence from rice spikelet bases from China suggest a comparable rate of evolution, in which non-shattering took a *minimum* of 1,500–2,000 years to evolve (Fuller et al. 2009). Such data support the suggestion that domestication took place far slower and with far weaker artificial selection than assumed in previous short gestation models (Purugganan and Fuller 2009, 2011) or that selection was discontinuous and not uniformly directional during the domestication period (Fuller et al. 2010a).

Prior to the study reported here, however, domestication rates have not been systematically calculated. In evolutionary biology two measures, the *darwin* (Haldane 1949) and the *haldane* (Gingerich 1993), have been developed to quantify rates of phenotypic change in contemporary micro-evolutionary studies (Grant and Grant 1995; Reznick et al. 1997; Hendry and Kinnison 1999; Kinnison and Hendry 2001; Bone and Farres 2001; Schoener 2011) as well as in palaeontology (Roopnarine 2003; Gingerich 2001). In the present study we calculated both darwins and haldanes from archaeobotanical data, including five Near Eastern crops and crops from elsewhere in the world. These calculated rates allow us to compare rates of evolution between plant domestication traits and those documented in other biological studies (Purugganan and Fuller 2011), as well as between crops in the Near East and elsewhere, between cereals and pulses, and between different traits within the same crop, such as grain size and non-shattering.

These comparisons provide a basis for a thorough quantitative comparison of various crop domestication patterns and for discussing similarities and differences in selection processes during domestication.

Materials and methods

In order to calculate rates of evolution we compiled available data on either seed-shattering/non-shattering or grain size measurements from several crops in different world regions. We consider non-shattering and grain size as the two traits of the domestication syndrome which are most amenable to archaeobotanical study, although we are aware that other traits, such as in growth habit and germination traits are important components of the domestication syndrome (Fuller 2007; Fuller and Allaby 2009; Abbo et al. 2010b). In total we found evidence from 11 crop species that were suitable for analysis, including examples from Asia, Africa and North America. The largest datasets were available from the Near East, where grain size data were compiled for 3 cereal and 2 pulse species (*Hordeum vulgare, Triticum monococcum, T. dicoccum, Pisum sativum, Lens culinaris*). Figure 1 shows the Near Eastern sites which have been considered in this study. In addition, we compared them to data from two other cereals, *Pennisetum glaucum* from West Africa and *Oryza sativa* from China, and the legume mungbean (*Vigna radiata*) from India. Also from China we have data on melon seed size increase. From North America we considered *Helianthus annuus* and *Iva annua*, for which achene size data are available (Asch and Asch 1985). The dataset and primary data sources are provided in the Electronic Supplementary Material (ESM).

For cereal grain size we looked at grain breadth (width) and thickness (height), since changes in grain length have proved less informative in previous archaeobotanical studies (e.g. Colledge 2001; Willcox 2004; on rice, Fuller et al. 2010b). Recent genetic research has indicated that grain width is under separate genetic control from grain length in wheat (Gegas et al. 2010) and rice (Shomura et al. 2008), and these traits appear to have been selected for during domestication. For other species, pulses and oilseeds, seed or achene length was considered.

In total the archaeological data for the 11 species come from 60 sites, with the largest dataset coming from Near Eastern species (5 species from 31 sites, but each site does not have data for all species or traits). The sample size of the number of measurements/specimens for various traits and taxa is summarized in Table 1. We focus our analysis on the time during which domestication took place. In this context we define the domestication period as the time over which a species became fully dependent on human action for dispersal, through the development of the non-shattering habit. As this is documented directly only for the cereals, we have assumed a similar time span for other species for the purpose of data compilation. For the Near

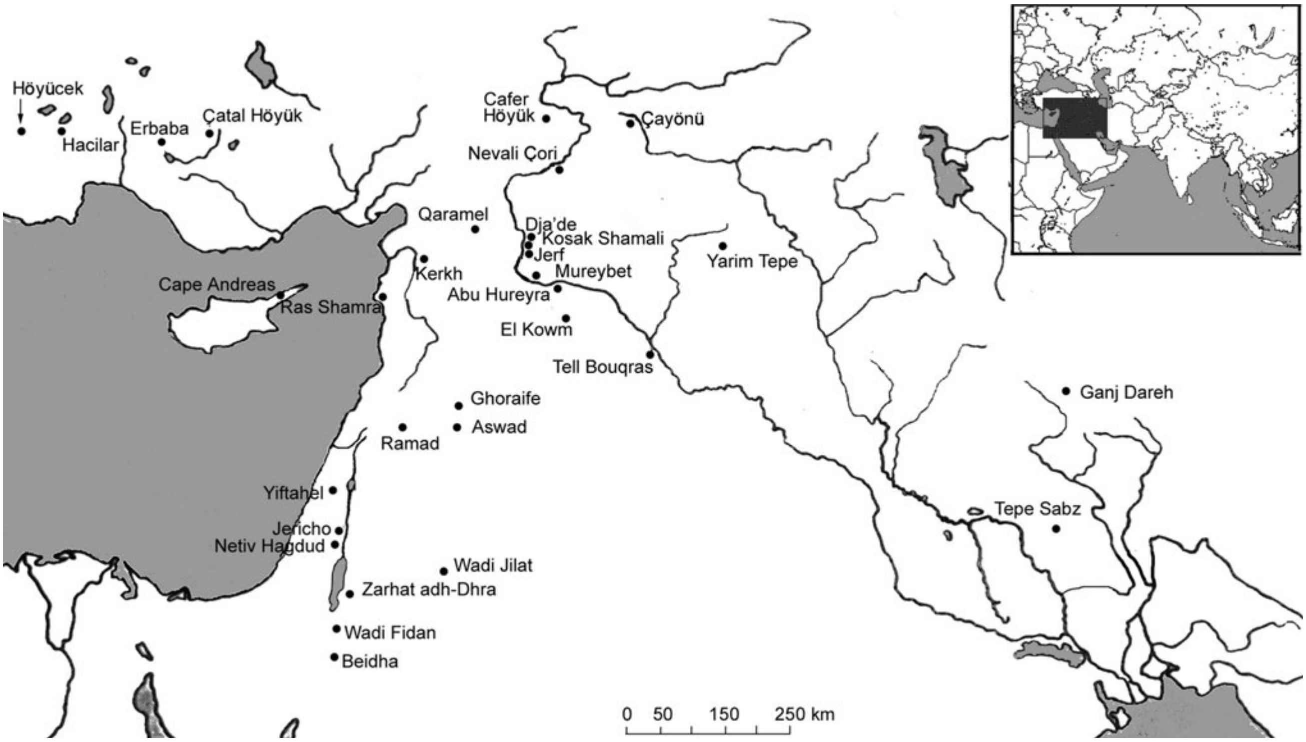

Fig. 1 Map of Near Eastern sites contributing evidence

Table 1 Dataset considered

Species	Seed size dataset (breadth)	Other metrics	Rachis dataset
Near Eastern taxa			
Hordeum vulgare	$n = 780$, $s = 11$	Thickness	$n = 4{,}186$, $s = 9$
Triticum monococcum	$n = 1{,}200$, $s = 11$	Length	$n = 1{,}381$, $s = 6$
T. diococcum	$n = 1{,}036$, $s = 10$	Thickness	
Lens culinaris (diameter)	$n = 1{,}471$, $s = 15$		
Pisum sativum (diameter)	$n = 2{,}945$, $s = 10$		
Other regions			
Oryza sativa	$n = 1{,}235$, $s = 17$	Thickness	$n = 2{,}640$, $s = 3$
Pennisetum glaucum	$n = 640$, $s = 6$	Thickness	
Vigna radiata	$n = 115$, $s = 6$	Length	
Cucumis melo	$n = 462$, $s = 7$	Length	
Iva annua		Length ($n = 556$, $s = 3$)	
Helianthus annus	$n = 157$, $s = 5$		

n total number of recorded specimens, *s* number of sites/phases providing data

East we have focused on data between 10000 and 6000 B.C. and the distribution of datasets by period and species is indicated in Table 2. A previous examination of barley grain metrics from this region over a longer time period (including Bronze Age and Iron Age datasets) suggests that increase in grain breadth and thickness stopped after the Late Pre-Pottery Neolithic B, with no significant or noticeable trends observed in later periods (Fig. 7.10 in Fuller and Allaby 2009). Therefore we consider it justified to stop our time series in the Late PPNB or earliest Pottery Neolithic for the Near Eastern crops. Similar 4,000-year windows have been used for other crops adjusted to when domestication is thought to have occurred in the relevant region. While 4,000 years is slightly longer than previously cited estimates, which are mainly between 3,000 and 1,000 years (Tanno and Willcox 2006; Weiss et al. 2006; Fuller 2007; Fuller et al. 2009), a 4,000-year window can reasonably be expected to capture most of the process of change. We focused only on the general region of domestication, except in the case of pearl millet where we have included one early site from India.

In general we have only used data from archaeobotanical assemblages in which a trait was measured in greater than 10 samples, and we required a minimum of at least 3 time points available during the domestication period in order to produce a regression line of domestication rate. When sufficient data were available from more than one phase of a site, we have included these phases as separate data points. However, in the case of sunflower we had only six measurements for the Late Archaic period (ca. 2500 B.C.), which included combining those from Napoleon Hollow and Koster level 6 (cf. Asch and Asch 1985).

In order to put data into time series it was necessary to have point age estimates for each assemblage. We did this by calculating a median or modal age for each site/phase considered as illustrated in the example in Fig. 2. For Near Eastern sites this involved compiling published radiocarbon dates, and calculating a sum of calibrated probability using the "sum" function in OxCal (Bronk Ramsey 2005). OxCal Version 3.9 was used but with the revised IntCal09 calibration dataset (Reimer et al. 2009). From the resulting probability distribution we have taken a modal age if there is a single strong modal peak in probability, or else a median age based on the 1σ distribution of probability. This is described in detail in the electronic supplement of Purugganan and Fuller (2011), which addresses the dating for each of the Near Eastern sites and shows the probability distribution of summed dates; most dates were taken from the compilations of Bischoff et al. (2006) and Thissen et al. (2007). For regions outside the Near East we have taken median dates for the general period of the material based on recent archaeological literature. For example, for rice we followed the dating estimates in the database of Fuller et al. (2010b), while for South India (mungbeans) the chronology followed the revised scheme of Fuller et al. (2007). For pearl millet an updated database of finds and dating evidence is provided by Manning et al. (2011). In the case of the North American data we have retained the conventional period dates provided by Smith (1992).

The *darwin* is defined as one logarithmic increase in the phenotypic value of a trait for each million years of evolution (Haldane 1949). This relies on population means and does not account for range of variation within the population. This is given by the equation

$$\mathrm{darwins} = [\ln(x_2) - \ln(x_1)]/[t_2 - t_1]$$

where x_1 and x_2 are the mean trait values at time points t_1 and t_2, respectively, in millions of years (Haldane 1949). We fit least-squares linear models of the natural logarithm of the trait values against time in millions of years, and the slope was used as the evolutionary rate estimate. An error margin was calculated based on the standard error of the

Table 2 Distribution of data across periods and taxa, for Near Eastern examples

	PPNA 10,500–8600 B.C.	EPPNB 8800–8200 B.C.	MPPNB 8200–7500 B.C.	LPPNB 7500–6200 B.C.	PN 6200–5500 B.C.	No. of sites/phases
Barley (rachis)	Netiv Hagdud	Aswad		Abu Hureyra		9
	ZAD 2			Wadi Fidan A & C		
				Ramad		
				Çatalhöyük		
				El Kowm II		
Barley (grain)	Mureybet	Jerf el Ahmar (late)	Ganj Dareh	Ramad	Yarim Tepe	11
	Jerf el Ahmar (early)	Dja'de		Bouqras		
	ZAD 2	Aswad		Ras Shamra		
Einkorn (spikelet base)	Qaramel	el-Kerkh	Cafer Höyük	Çatalhöyük		6
		Nevalı Çori				
Einkorn (grain)	Qaramel, Mureybet, Jerf el Ahmar (early)	Jerf el Ahmar (late)	Wadi Jilat 7	Ramad	Höyücek	11
		Dja'de		Erbaba		
		Çayönü		Cape Andreas		
Emmer (grain)		Dja'de		Ghoraifé	Höyücek	10
		Çayönü		Ramad I & II	Yarim Tepe	
		Aswad		Erbaba	Kosak Shamali	
Lentil (seed)	Mureybet	Nevalı Çori	Ganj Dareh	Ras Shamra	Erbaba	15
		Aswad	Beidha	Ramad	Ras Shamra	
			Yiftah'el		Höyücek	
			Jericho		Jericho	
					Tapi Sabz	
					Çayönü	
Pea (seed)	Mureybet	Jericho	Hacilar	Ramad (2)	Erbaba	10
		Çayönü	Ghoraifé			
		Aswad				
No. taxa-traits/sites	6/5	7/8	5/8	7/14	5/8	

regression line. The trait value for non-shattering is the frequency of non-shattering rachises/spikelet bases.

The *haldane* is the change of one standard deviation of a trait value per generation (Gingerich 1993). As such this rate takes into account the range of variation within assemblages. In addition, rather than an arbitrary 1 million-year time scale, this unit is scaled to the turnover of the organism. However, in this case since the crops are all annuals, this was simply held constant as 1 year. Evolutionary rates in haldanes is given by the equation

$$\mathrm{haldanes} = [\mathrm{x}/\sigma] = [(\mathrm{x}_2 - \mathrm{x}_1)/\sigma_\mathrm{p}]/[\mathrm{t}_2 - \mathrm{t}_1]$$

where x_1 and x_2 are the mean trait values at time points t_1 and t_2, respectively, in generations and σ_p is the pooled standard deviation for the trait across the time points (Gingerich 1993).

In grain size data, where standard deviations are not reported we estimated standard deviation from the range of measurements (from the minimum to the maximum) and the sample size on the assumption of a normal distribution. The conversion factor is from Table 27 in Pearson and Hartley (1976) multiplied by the difference of the observed maximum and minimum. In some cases we have combined data from several samples from the same site, and calculated a weighted mean, and then obtained the standard deviation by the same formula based on the total number of specimens.

In the case of non-shattering, we have used the presence of indeterminate rachises to bracket the most likely proportion of non-shattering (domesticated) types and calculate a standard deviation around that. By ignoring all indeterminate rachises we derived a point estimate of the average domesticated fraction. Then, by treating the indeterminate rachises in turn as either all wild-type or all non-shattering, we obtained a maximum and minimum estimate of the possible domesticated fraction. Based on the range between these estimates and the overall sample size we have derived a standard deviation based on the normal distribution (i.e. Table 27 in Pearson and Hartley 1976).

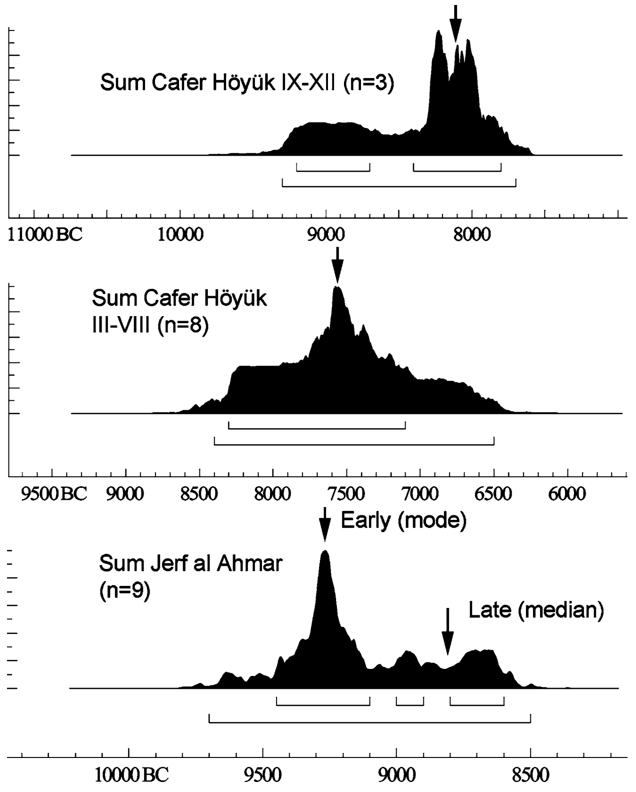

Fig. 2 Examples of estimating age by modal and median value of summed calibration probability

In the case of rice, averages and standard deviations for non-shattering could be calculated directly from multiple archaeological context samples representing the same phase (as in Fuller et al. 2009). For calculating haldanes we needed a pooled standard deviation for non-shattering. This is given as

$$\sigma_p = \{ [\Sigma(n_i - 1)(\sigma_i)^2]/[\Sigma(n_i - 1]\}^{1/2}$$

where σ_i and n_i are the standard deviation and sample size for timepoint i, respectively, and we sum all timepoints. We also fit least-squares linear models to obtain the evolutionary rate estimate.

Results and discussion

There is a clear trend for domestication indicators to increase over time in all of these datasets. But we find variation in rate estimates across species and between non-shattering and grain size change (Table 3).

Non-shattering

Starting with non-shattering, it can be seen that there is a strong regression line, with a very similar slope generated by both the barley and einkorn non-shattering data (Fig. 3). It should be noted that we have only included sites that had some presence of non-shattering rachises and sites with entirely wild-type assemblages (e.g. Jerf, Dja'de) have been left out, although they indicate that the start of this evolutionary trend was indeed slow, and may not have been uniform across all local populations of early cultivated cereals. In addition, sites from Cyprus that have small quantities of domesticated cereal chaff reported (Colledge 2004) have not been included, as these may have been prone to exceptional ecological conditions arising from their island context; this indeed appears to be the case with grain size in einkorn which increases rapidly on Cyprus by comparison to the mainland (Lucas et al. 2011). These charts also indicate how sparse good quantitative evidence still is for the Near East as whole; it is not yet possible to track local area trends and to compare change across different areas of the Near East. Nevertheless, the data do appear to suggest that cereals in the Near East as a whole constitute an interacting meta-population that was undergoing evolution towards non-shattering over a protracted period of time. As illustrated previously (Fuller et al. 2009, 2010a; Purugganan and Fuller 2009) the data for rice spikelet bases show a very similar rate of increase. This is despite the fact that rice domestication was taking place in a different cultural context, and may have had higher levels of cross-pollination between wild and cultivated populations. This suggests that the main driving forces in this process—selection pressures from cultivation and harvesting, balanced against wild progenitor adaptations and gene flow—were broadly comparable for different cereal domestications (Fuller 2007).

The conversion of this evidence to evolutionary rate units produces broadly similar results across the different species (Table 3; Fig. 4). The estimated rates in darwins are correlated with the time to fixation of the trait, with high rates for both barley (~944 darwins) and rice (~1,160 darwins), while einkorn wheat evolved more slowly, about half as fast (~533 darwins) (see Table 3). Relative to the standard deviation in trait values, however, it appears that all three cereal crop species have similar evolutionary rates (0.8–1.3 × 10^{-3} haldanes) (Fig. 4). In archaeological data for wheat and barley, several spikelet bases/rachises were reported as indeterminate. While these have been used to compute an error on the graphs in Fig. 3, we have ignored them in the calculation of evolutionary rates. If instead we assume that they represented either wild or domesticated phenotypes, the rate estimates (~990 darwins if indeterminate rachises are classed entirely as domesticated, and ~786 darwins if they are classed as wild) are fairly similar to the calculated evolutionary rate, when we ignore the indeterminate spikelet bases. Thus they do not impact our general conclusions.

Table 3 Results of evolutionary rate estimates for all taxa and traits

Species	Trait	Darwins	r^2	Haldanes ($\times 10^3$)	r^2
Cereals: rachis					
H. vulgare	Non-shattering	943.8	0.77**	1.3	0.81***
T. monococcum	Non-shattering	532.8	0.59*	0.9	0.79*
O. sativa	Non-shattering	1159.6	0.94	0.8	0.96
Cereals: size					
H. vulgare	Breadth	125.7	0.77***	1	0.77***
H. vulgare	Thickness	152.9	0.69**	1.2	0.68**
T. monococcum	Length	128.7	0.65**	0.8	0.62**
T. monococcum	Breadth	169.3	0.88***	1.2	0.89***
T. dicoccum	Breadth	36.5	0.28	0.3	0.29
T. dicoccum	Thickness	58.3	0.59**	0.4	0.59**
O. sativa	Breadth	71.6	0.54***	0.5	0.54***
O. sativa	Breadth	45	0.12	0.3	0.13
P. glaucum	Breadth	123.1	0.28	0.6	0.25
P. glaucum	Thickness	235.7	0.77	n.a.	n.a.
Pulses: size (assumes 4,000 year domestication period)					
L. culinaris	Length	57.3	0.28	0.4	0.26
V. radiata	Length	186.6	0.18	1.6	0.19
V. radiata	Breadth	171	0.18	1.6	0.16
P. sativum	Length	13.6	0.03	0.05	0
Pulses: size (assumes 2,000 year domestication period)					
L. culinaris	Length	129.2	0.38	1.3	0.37
V. radiata	Length	729.5	0.42	8.3	0.54
V. radiata	Breadth	827.4	0.61	9.5	0.69*
P. sativum	Length	133.8	0.69*	3.2	0.82*
Others: size					
I. annua	Length	154.4	0.95	1	0.98*
H. annus	Breadth	114.6	0.82*	0.6	0.75*
C. melo	Length	265.2	0.5	1.8	0.49
C. melo	Width	376.8	0.52	2.3	0.52

Statistical significance for r^2 is indicated: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Grain size

Grain size shows a clear increase with domestication across species. While there is a great deal of variation in how much grain size change there was, ranging from about 25–30% increase in grain breadth in emmer and rice to an 80% increase in pearl millet and a 100% increase in mungbean seed length (Fig. 5), the upward shift is seen in population averages, as well as maximum sizes and minimum sizes (Figs. 6, 7). A cleaner linear trend is seen in the cereal data (Fig. 6). Similar trends are apparent in oilseeds (*Helianthus, Iva*), melon and most pulses (Fig. 7) although the increase in pulses and melons does not appear that straightforward. As we explore below, this may be because size change took place over a shorter period in pulses and melon, i.e. it was faster, and therefore they need to be represented over a shorter time period than the arbitrary 4,000 years used for evolutionary rate estimates. In order to take this into account we also calculated the evolutionary rate for the legumes using a 1,000 or 2,000-year domestication period (Fig. 8), since this visually appears to capture the period of most marked change in lentils, while other pulses possibly had even shorter periods.

It should be noted that einkorn grain measurements from some PPNA sites (Mureybet, Jerf el Ahmar, Dja'de) included grains of rye (*Secale* sp.) since these taxa are difficult to separate on morphological grounds, and these sites contained rye chaff (Willcox and Fornite 1999; Willcox 2004). Nevertheless exclusion of these assemblages would make little difference to the overall trend or rate estimate.

We have not made any adjustments for the potential impact of carbonization. While it is well-known to archaeobotanists that grains tend to undergo shrinkage during carbonization, perhaps often on the order of 10–20% (cf. Willcox 2004; Zohary and Hopf 2000; Braadbart and Wright 2007), we have assumed that this has affected all

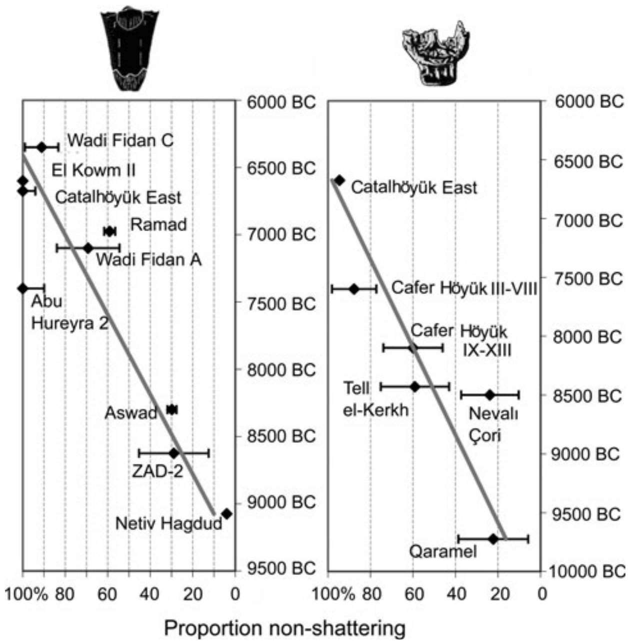

Fig. 3 The increase in the proportion of domestic-type raches/spikelet forks in barley and einkorn. These data exclude sites that have no reported domesticated types (such as Jerf el Ahmar), and Wadi Jilat 13 which has an anomalously high percentage of wild barley (>90%) for the Late PPNB. The mean represents the portion of non-shattering to shattering, excluding indeterminate specimens, while the standard deviation is estimated by taking into account the indeterminate specimens and sample size

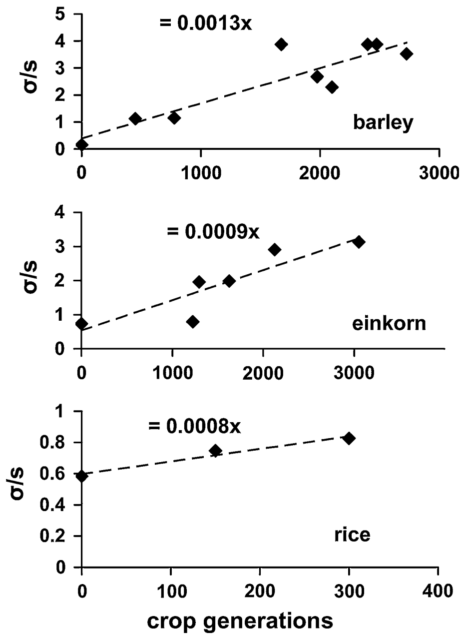

Fig. 4 Haldane rate estimates for the evolution of non-shattering in barley, einkorn and rice

assemblages more or less equally, and whatever variation there might be has simply added additional noise to the data. In other words, we assume that the effects of carbonization are random with respect to our temporal trends, i.e. there was no directional change in charring conditions. Since we are not comparing the archaeological metrics to modern baselines, a precise conversion factor for shrinkage is not necessary.

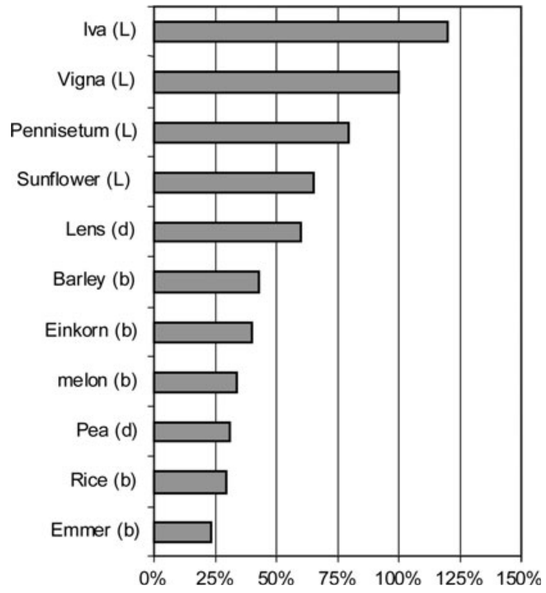

Fig. 5 A comparison of the total amount of seed size change, as represented by the percentage increase in grain width over the entire domestication period

It is possible that phenotypic plasticity to the more favourable environments of cultivated fields may be responsible for some grain size increase (as suggested by Willcox et al. 2008 for explaining the shift between the PPNA and Early PPNB assemblages at Jerf el Ahmar). Phenotypic plasticity is unlikely to account for the directionality of trait phenotypes over the entire protracted time period of the domestication process, although improved cultivation techniques during this time span may have contributed to the observed trend. Moreover, genetic studies have shown that the phenotypes we study have a large genetic component, i.e. high heritability (Kato 1990; Young 1991; Gu et al. 2005; Fox et al. 2006; Sadras 2007), thus indicating that phenotypic differences are more likely to have a strong genetic basis. Recent genetic work has identified important genes involved in increasing grain breadth in domesticated rice (Shomura et al. 2008) and wheat (Gegas et al. 2010).

Wheat and barley grains start showing increases in size from the PPNA and early PPNB approximately 11100–10500 B.P., as observed in Jerf el Ahmar in Syria (Willcox 2004) and ZAD-2 in Jordan (Meadows 2004; Edwards et al. 2004). Other species, however, such as *P. glaucum* and *V. radiata* (Fuller 2007) show increases in grain size later in the domestication period. Indeed, recent evidence from Mali indicates that non-shattering was well-established between

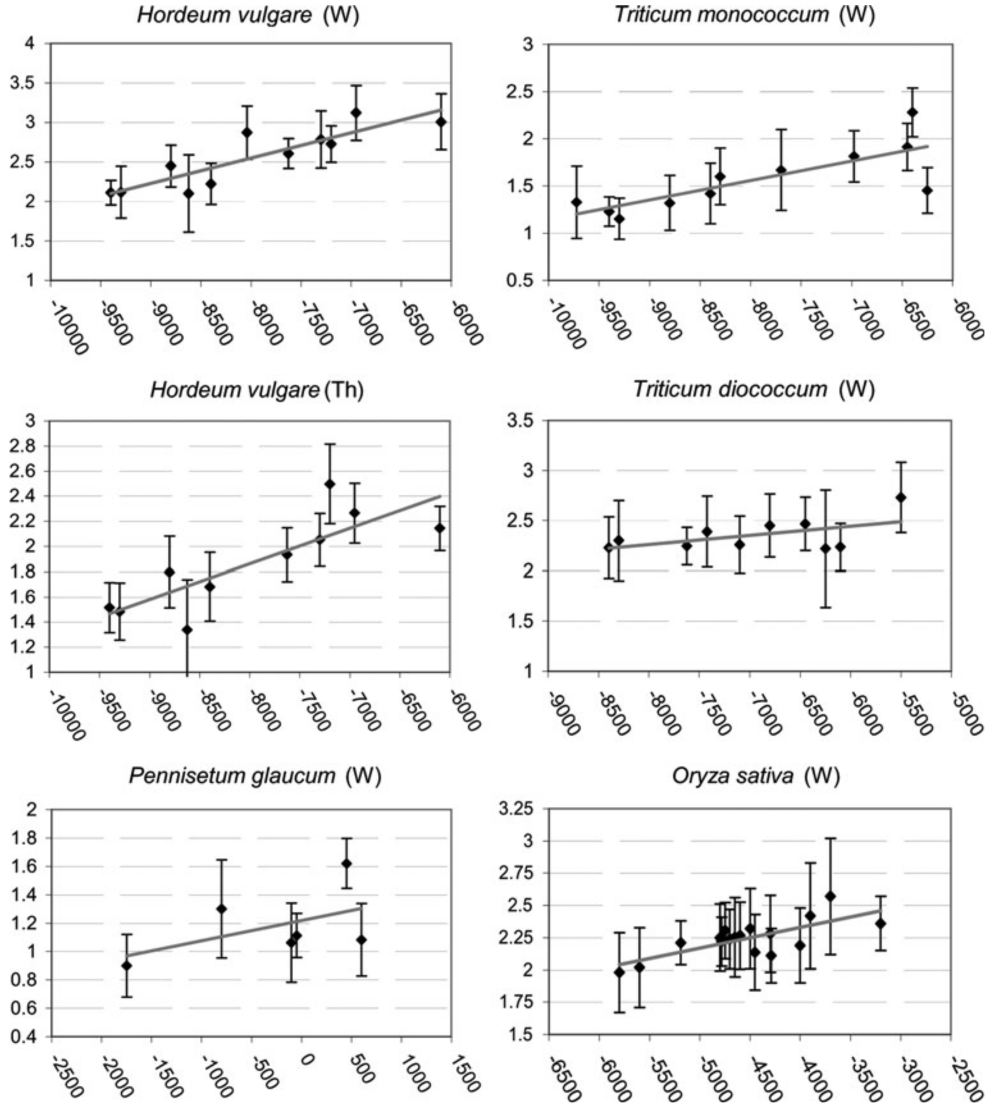

Fig. 6 Charts of cereal population grain sizes over time, with linear regression trend lines shown

2500 and 2000 B.C. before there is any evidence from grain size change in the region (Manning et al. 2011).

Like non-shattering analysis, the fit of the data is generally good (see Table 3; Figs. 6, 7), with 9 of the 18 estimates having r^2 values >0.5. The data from cereal crops are generally better, with a significant fit ($P < 0.01$) for most of the estimates. Almost all species showed evolutionary increases in grain/seed size during domestication, with most having rates ranging from ~50–350 darwins and $0.3–2.3 \times 10^{-3}$ haldanes (see Table 3). Absolute rates in terms of darwins were significantly slower in grain size than for non-shattering. However, it is possible that these differences are influenced by the use of different kinds of units, i.e. grains have measurements; non-shattering is a percentage (see discussion in Purugganan and Fuller 2011). However, in haldane units it is clear that rates of evolution appear broadly comparable, especially across cereals and lentils, of the same order of magnitude and often of very similar rate (Fig. 8). When shorter time windows of domestication are assumed for the lentils and peas, evolutionary rates change substantially (Fig. 8, bottom). For lentils the first 2,000 years of seed size change show a rate of change 1.3×10^{-3} haldanes, comparable to the rate in thickness change for einkorn and barley over the entire 4,000 years, while the 4,000-year estimate for lentil is only 0.4×10^{-3} haldanes, comparable to grain size change for emmer. Thus regardless of the time length of the frame of reference, lentil size change rates are comparable in magnitude to cereals. Only in the case of pea does a 4,000-year frame fail to capture much evolutionary change, presumably because pea evolution shifts towards varietal differentiation after domestication. However, a shorter window of 2,000 or 1,000 years (shown here) captures a high rate of directional change.

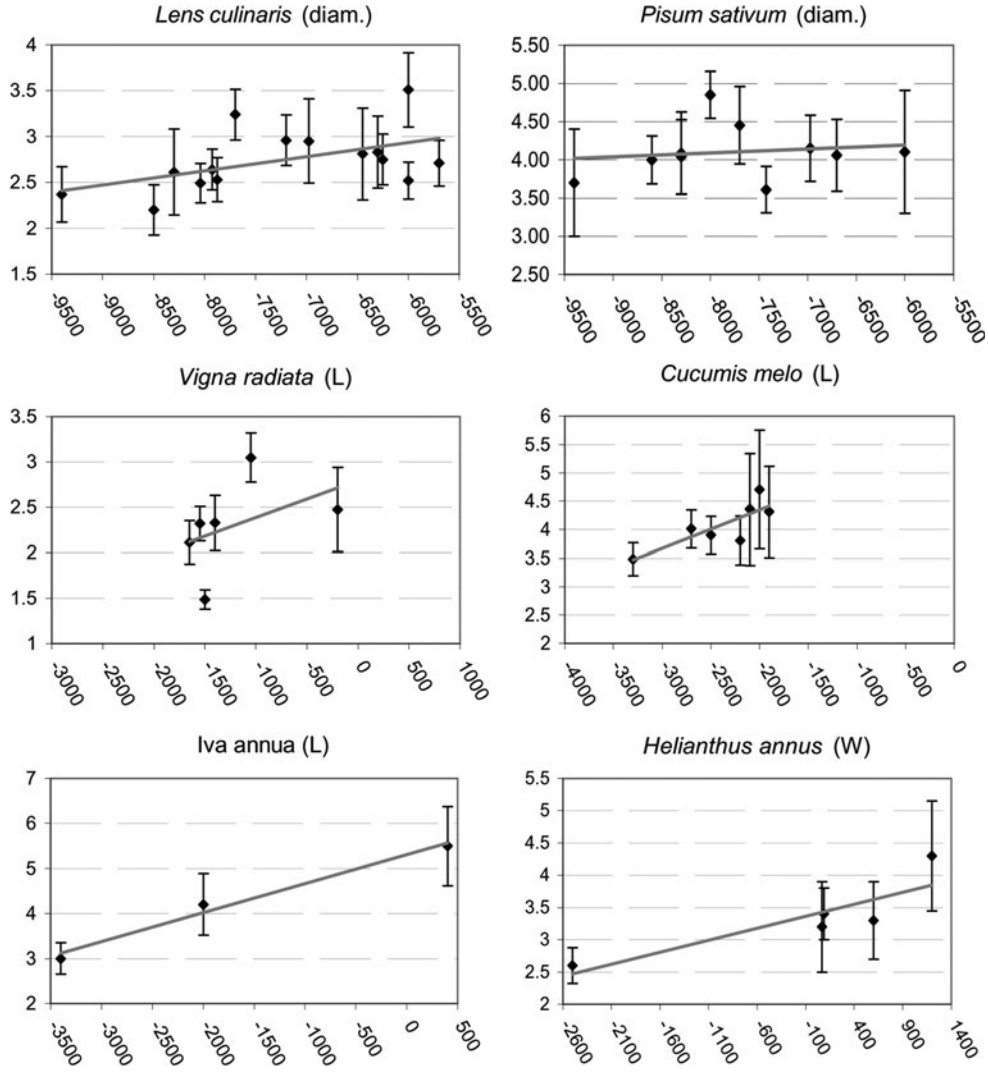

Fig. 7 Charts of non-cereals seed sizes over time, with linear regression trend lines shown

Comparisons across crops and to "natural" evolution

The calculation of darwins and haldanes provides a means of comparing phenotypic change across species. This provides a basis for contrasting different crops or the change in different domestication characters in the same crop. In addition, it allows for addressing the question of how similar evolutionary rates are under domestication as compared to "natural" evolution recorded in various biological studies. Figure 9 represents one way of visualizing comparisons by way of a scatter plot of change in averages (darwins) versus change in overall populations (haldanes). In order to represent "natural" evolution we have plotted the means and medians in all plant studies as compiled by Bone and Farres (2001) and animal studies (Kinnison and Hendry 2001). Based on the expanded dataset of Hendry et al. (2008) we have taken the mean and median values of wild animal evolution. As can be seen, the calculated rates of change in domestication traits plot within the rate space defined by the averages of wild plant and animal studies. As noted in Purugganan and Fuller (2011), rates of change under domestication appear to be somewhat on the slow end of the 'typical' range represented by modern evolutionary studies. Nevertheless our basic conclusion is that domestication traits change at rates broadly comparable to "natural" evolution. This also provides a baseline for identifying instances of faster trait evolution, such as in island contexts (see Lucas et al. 2011).

Figure 9 also allows some observations on contrasts between individual traits and crops. Thus non-shattering data fall on the higher end of rates of change by comparison to grain size, although this is most evident in darwins, reflecting only changes in the mean. Cereals and other crops show comparable rates of change in seed size characters, although pulses appear generally at the slower end when a 4,000-year domestication window is assumed. If the window is reduced to 2,000 years pulses look much faster, especially the mungbean. Such variation suggests

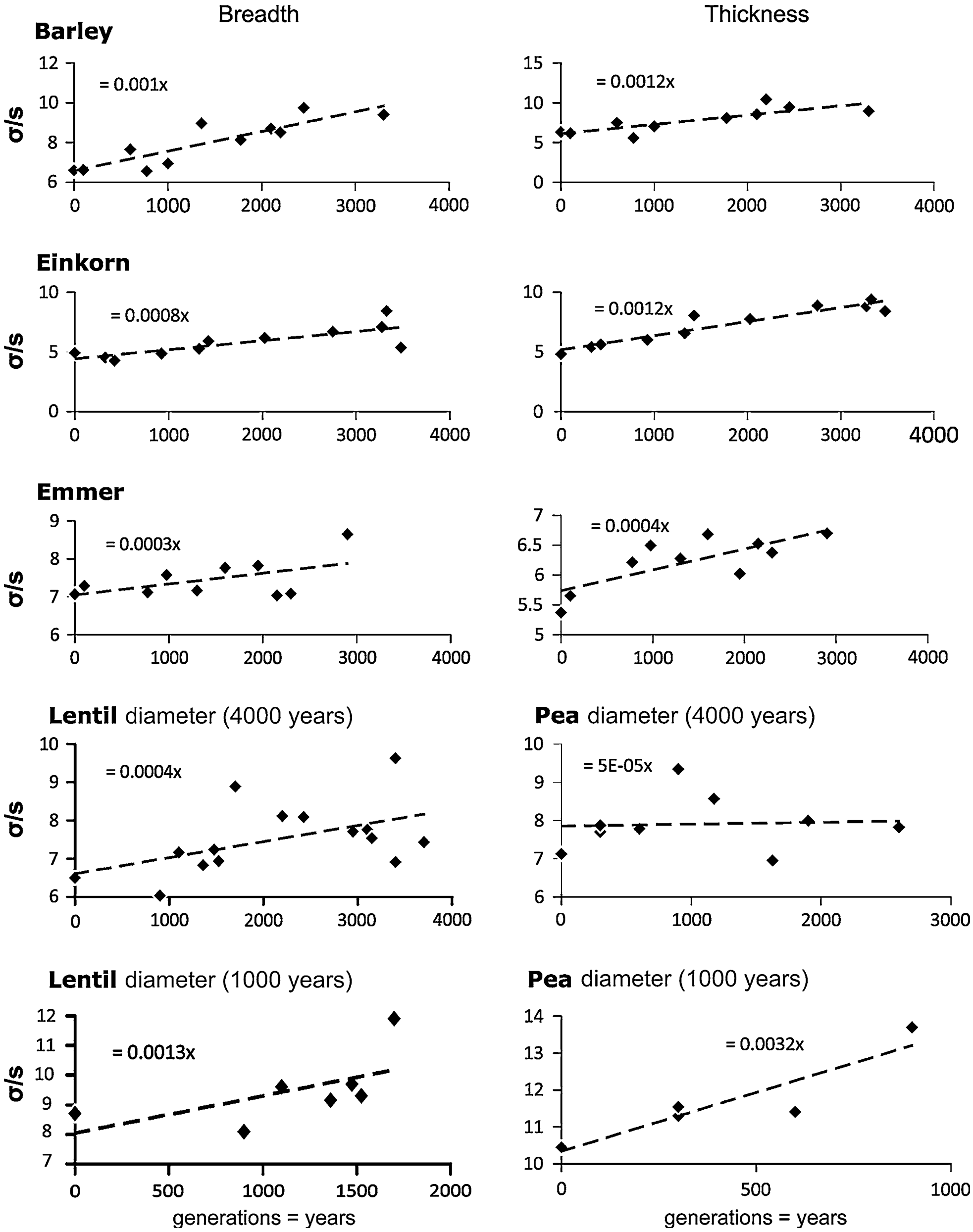

Fig. 8 Haldane rate estimates for the evolution of larger grains in selected Near Eastern domestications. These data show rates calculated separately from grain breadth and grain thickness data for cereals, and diameter of lentils and peas. For pulses shorter domestication periods are also proposed, in which the rate is calculated from the shortest period (rounded to millennium) that captures all the size increase in the dataset. Equations on each graph indicate the haldane rate taken as the slope of the regression line

that it is necessary to explore the impact of varied domestication windows, and how these could be better derived empirically.

Conclusions

This study demonstrates that archaeobotanical data provide a reliable fossil record of the nature and rate of the evolutionary changes that crops underwent during domestication. Despite the patchiness of the archaeobotanical data, they provide quantifiable evidence for the response of plant populations to the selection pressures of early cultivation. Nevertheless, some of the limitations of current evidence must be noted. Obviously, some domestication traits (such as growth habit, evenness of ripening, and germination patterns) are not readily preserved in archaeological specimens. We are limited mainly to two traits: seed size and seed dispersal. Given that data for a single species may arise from archaeological sites found in various geographic locations, an underlying assumption is that materials from disparate sites are representative of species-wide evolutionary patterns and not local diversification. This is valid if there is sufficient gene flow between populations so that selection for observed phenotypes is manifested across the species range (Feldman and Kislev 2007; Allaby et al. 2008; Allaby 2010); given that we use data geographically limited to the domestication centre of origin in its broad

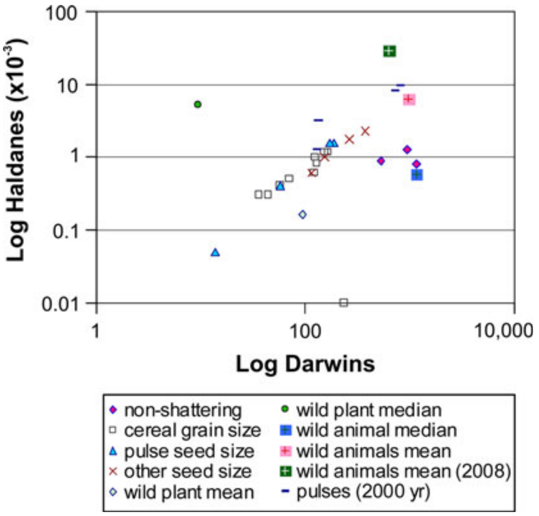

Fig. 9 A comparison of evolutionary rates (Darwin and Haldane units) under domestication across crops and traits, with comparisons from typical evolutionary rates from other biological studies (Kinnison and Hendry 2001; Bone and Farres 2001; Hendry et al. 2008). Rates for pulses are shown for both 4,000 and 2,000-year domestication episodes

sense, i.e. the Fertile Crescent, we feel this is a reasonable assumption. The high r^2 values for most of our regression lines also suggest that we are looking at a coherent process, especially for the cereals. Obviously, it would be ideal to look at rates of change within more restricted regions, such as the Damascus Basin, the Jordan Valley or the Upper Euphrates, but the sum of the available data is still too limited for any such regional studies. Furthermore, we cannot necessarily infer that the domestication process was uniformly linear and directional, and that within some periods and regions metastable states of semi-domestication might have existed (see Fig. 4 in Fuller et al. 2010a).

There remain many uncertainties that we are unable to address at present. For example, we have taken arbitrary time periods of 4,000 or 2,000 years to capture the period of domestication, rather than arriving empirically at how long domestication took. Our expectation is that during the domestication process selection will be unidirectional and rates of change may approximate a linear progression, but there will continue to be selection pressures, such as adaptation to local conditions and selection for varietal diversification after the initial period of domestication. We might therefore expect a period of rapid rate change followed by a reduced rate of change and greater variation around the linear regression line. Such patterns have been found for example when comparing shorter term (~20 generations) and longer term (~100 generations) experimental selection for high oil content in maize (see Fig. 3 in Bone and Farres 2001).

We also remain uncertain about how long to regard the pre-domestication cultivation phase to have been. While sites in which the majority of cereals were still non-shattering can be regarded as showcasing pre-domestication cultivation, so too can sites without any clear morphological domestication indicators, but with evidence of arable floras (Willcox et al. 2008, 2009; Willcox 2011). They may represent pre-domestication cultivation but of a different sort or stage from when there is directional selection for domestication traits.

For pulses, it is not yet possible from archaeobotanical evidence to determine whether loss of wild-type germination inhibition (a key trait in pulse domestication: see Abbo et al. 2010b; Fuller and Allaby 2009, pp. 258–259) evolved prior to grain size increase, although it is logical that it might have done so or begun to do so. Abbo et al. (2010b) demonstrate experimentally that a lack of germination in wild *Pisum* must be overcome in order to have a reasonable yield. This could either be by selecting a freely-germinating mutant that existed in the wild (see also Ladizinsky 1993), or by physically abrading seeds, for example in a mortar, in a way similar to that of the experiment by Abbo et al. (2010b). Reduced hard-seed dormancy consistently differs between modern domesticates, as do other domestication traits such as seed size, growth and pod dehiscence (Weeden 2007). Archaeobotanical evidence for seed size indicates that at least this aspect of the domestication syndrome evolved gradually.

As recent theory building on the processes of coevolution suggests, co-evolutionary relationships take place as a mosaic of differing pulls and pushes across geographic space, i.e. there is a geographic mosaic of coevolution (Thompson 2005). Geomosaic theory would postulate that there were "hotspots" with higher selection for domestication, e.g. around intensively cultivating communities who routinely practised sickle harvesting, and "coldspots", e.g. wild stands and areas of predominantly hunter-gatherer lifestyles, as well as locations in between, and gene-flow between these areas (see Allaby 2010). However, until we have much denser data points both in time and space it is impossible to pinpoint potential hotspots and coldspots. Nevertheless, the current geographic spread of data points both in time and in space suggests that the evidence does not fit the conventional orthodoxy of a rapid local domestication process occurring in a single core area or a "golden triangle," followed by dispersal to other regions (e.g., Kozlowski and Aurenche 2005; Honne and Heun 2009; Abbo et al. 2010a; Haldorsen et al. 2011).

It is worth thinking through some of the cultural practices that might have contributed to "lukewarm" or "cool" spots. These could have been areas near human communities, rather than wild stands, but where cultivation was not contributing strongly to selection for domestication traits. For example, some villagers may have relied more heavily on wild gathering with more occasional and less intensive cultivation, perhaps without sickle harvesting, or have been experiencing regular crop failures. That the quantitative importance of cereals across sites in the Near East varied seems clear. For example, sites in the north-east Fertile Crescent have provided very limited evidence for wild progenitors or pre-domestication cultivation (Savard et al. 2006), and some of the earliest Euphrates sites of inferred cultivation have large quantities of potentially edible wild food plants (Willcox et al. 2009; Colledge and Conolly 2010; Wollstonecroft et al. 2011). Even at sites where pre-domestication cultivation is inferred (e.g. Jerf el Ahmar, ZAD-2, Netiv Hagdud, 'Iraq ed-Dubb) or where some morphological domestication traits have begun to occur in a few crops (e.g. Aswad, Çayönü, Ganj Dareh, Beidha) wild gathered foods, such as almond, *Pistacia,* small-seeded legumes, sedge nutlets (notably *Bolboschoenus glaucus*) and Polygonaceae nutlets are also prominent (Van Zeist and Bakker-Heeres 1985; Van Zeist et al. 1986; Van Zeist and de Roller 1992, 1995; Colledge 2001; Edwards et al. 2004; Willcox et al. 2009). Wild gathered plants had continued importance in many communities, as suggested by stores of these from Çatalhöyük (Fairbairn et al. 2007; Bogaard et al. 2009). As already suggested by Willcox et al. (2008) in some years cultivators may have bolstered their stores with wild material, i.e. injecting wild genotypes into their cultivated populations. It may be that some household or community traditions did this routinely. Alternatives to sickle harvesting have been proposed for some sites (e.g. Kislev et al. 2004; cf. Fuller 2007). As explored by Fuller et al. (2010a), the evolution of non-shattering forces people to add a threshing and winnowing stage to crop-processing before dehusking. In other words domestication involves not just morphological changes in the plant but also changes in human practices. Even though dehusking is the more onerous task, it may be that the extra labour involved in threshing could have acted as a disincentive for some households or communities intentionally selecting their incipient domesticates, and a return instead to periods of wild cereal gathering, or restarting cultivation from "uncontaminated"/"natural" seed corn.

The archaeobotany of domestication is more complex than merely determining whether or not domestication/agriculture was present/practised. There remains much more research to be done, not just to gather more data from more sites and periods, but also to think through how we can use these analytically to shed light on protracted processes and regional processes as well as local, on-site activities, and ultimately to tease out the inter-relationships between the local and the regional. Thinking explicitly about archaeobotanical evidence as a fossil record of domestication, and borrowing some of the tools of evolutionary biology, such as quantifying rates of phenotypic change, is one way to proceed, as we have illustrated in the present paper. Further work along these lines should aim to derive the shape of evolutionary rate change curves through more work on how rates in particular species and regions change, thereby defining rates of domestication empirically in order to transcend the arbitrary windows of 2,000 or 4,000 years.

Acknowledgments We are thankful to the peer reviewers of this manuscript for their constructive comments and criticisms. Some raw metrical data was provided to DQF by George Willcox, and some data was compiled by Mervyn Jupe as part of a student project.

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