ORIGINAL ARTICLE

doi:10.1111/j.1558-5646.2010.01093.x

ARCHAEOLOGICAL DATA REVEAL SLOW RATES OF EVOLUTION DURING PLANT DOMESTICATION

Michael D. Purugganan[1,2] **and Dorian Q. Fuller**[3]

[1] *Department of Biology and Center for Genomics and Systems Biology, 100 Washington Square East, New York University, New York, New York 10003*

[2] *E-mail: mp132@nyu.edu*

[3] *Institute of Archaeology, University College London, 31-34 Gordon Square, London WC1H 0PY, England*

Received January 8, 2010
Accepted June 30, 2010

Domestication is an evolutionary process of species divergence in which morphological and physiological changes result from the cultivation/tending of plant or animal species by a mutualistic partner, most prominently humans. Darwin used domestication as an analogy to evolution by natural selection although there is strong debate on whether this process of species evolution by human association is an appropriate model for evolutionary study. There is a presumption that selection under domestication is strong and most models assume rapid evolution of cultivated species. Using archaeological data for 11 species from 60 archaeological sites, we measure rates of evolution in two plant domestication traits—nonshattering and grain/seed size increase. Contrary to previous assumptions, we find the rates of phenotypic evolution during domestication are slow, and significantly lower or comparable to those observed among wild species subjected to natural selection. Our study indicates that the magnitudes of the rates of evolution during the domestication process, including the strength of selection, may be similar to those measured for wild species. This suggests that domestication may be driven by unconscious selection pressures similar to that observed for natural selection, and the study of the domestication process may indeed prove to be a valid model for the study of evolutionary change.

KEY WORDS: **Archaeobotany, artificial selection, darwins, haldanes, natural selection.**

Domestication is an evolutionary process of species divergence associated with a specialized mutualism, in which morphological and physiological changes result from the cultivation/tending of plant, animal or fungal species by a mutualistic partner (Diamond 2002; Zeder 2006; Purugganan and Fuller 2009). Some of the earliest examples of this unique coevolutionary mutualism include domestication of fungal species by ant and beetle cultivation, which appeared ~20–65 million years ago (Mueller et al. 2005). The most prominent cases, however, are the numerous domestications of plant and animal species by *Homo sapiens*, which began in the Neolithic agricultural revolution, ~10,000–13,000 years ago. Humans were initially tuber-, seed- and nut-gathering foragers over most of prehistory, but began to cultivate food plants starting in the Epipaleolithic/Neolithic Period, as it is defined archaeologically in various regions of the world (Barker 2006). Cultivation was a change in human behavioral ecology that transformed hunter–gatherer groups into sedentary agricultural societies that ultimately gave rise to current human cultures and led to the coevolutionary origins of domesticated crop plant and livestock animal species. (Diamond 2002; Zeder 2006; Purugganan and Fuller 2009). Archaeological evidence suggests that humans independently brought food plants into cultivation in 24 regions, and grain crops, mostly grasses, were the focus of early cultivation in perhaps 15 regions in both the Old and New Worlds (Purugganan and Fuller 2009).

Cultivation involves manipulation of the soil and vegetational environment and cycles of harvesting-storage that exerts selection pressures for recurrent adaptations on the part of cultivated species (Zeder 2006; Fuller 2007; Fuller et al. 2010). Charles Darwin used domestication as an analogy to evolution by natural selection (Darwin 1859), and ever since there has been strong debate on whether this process of recent, rapid species evolution in domesticated taxa, brought about by human association, is a valid paradigm for evolutionary study. It is not uncommon to view domestication as a special class of species diversification, distinct from species divergence via natural selection in the wild. There is a presumption, for example, that selection under domestication is strong (Innan and Kim 2004), and most models of plant domestication assume that this leads to rapid-to-very rapid evolution of cultivated species (Zohary 1969; Iltis 1983; Ladizinsky 1987; Hillman and Davies 1990; Honne and Heun 2009). Indeed, domestication is believed to occur in as little as a few hundred years (Hillman and Davies 1990), and this viewpoint informs evolutionary genetic analysis of domesticated taxa (Innan and Kim 2004; Zhang et al. 2009).

Alternatively, however, domestication can be considered simply as a form of animal/plant coevolution, conceptually similar to examples of evolutionary diversification driven by other multispecies interactions, with similar levels and patterns of evolutionary change to those observed in wild species (Purugganan and Fuller 2009). If we are to ascertain, however, whether rates of evolution are similar to or exceed those experienced by wild species under natural selection, it is necessary to measure phenotypic rates of evolution during the domestication process. This can be accomplished using two metrics of evolutionary rates developed to allow comparisons between species—the "darwin," defined as one logarithmic increase in the phenotypic value of a trait for each million years of evolution (Haldane 1949), and the 'haldane," which is the change of one standard deviation of a trait value per generation (Gingerich 1993). These two measures have been extensively used to quantify rates of phenotypic change in both contemporary microevolutionary studies (Grant and Grant 1995; Reznick et al. 1997; Hendry and Kinnison 1999; Bone and Farres 2001; Kinnison and Hendry 2001) as well as using paleontological data (Gingerich 2001; Roopnarine 2003).

Archaeological studies provide fossil data that temporally track phenotypes and trace microevolutionary dynamics that accompany speciation and selection during the evolution of domesticated taxa, allowing us to estimate evolutionary rates and strengths of selection. Although the archaeobotanical record preserves several phenotypic features, two traits in particular—rachis nonshattering in cereal crops and grain/seed size in seed crops—provide quantitative information on phenotypic evolution during domestication (see Fig. 1). The seed nonshattering trait is considered the key phenotypic indicator of domestication, particularly for cereal and legume species. The evolution of nonshattering is regarded as a hallmark of domestication, because the fixation of this trait reduces the ability for natural seed dispersal and is thus deleterious in wild populations and makes the cultivated species dependent on human intervention for continued reproduction (Harlan 1992; Purugganan and Fuller 2009; Fuller and Allaby 2010). Nonshattering evolves due to changes in harvesting

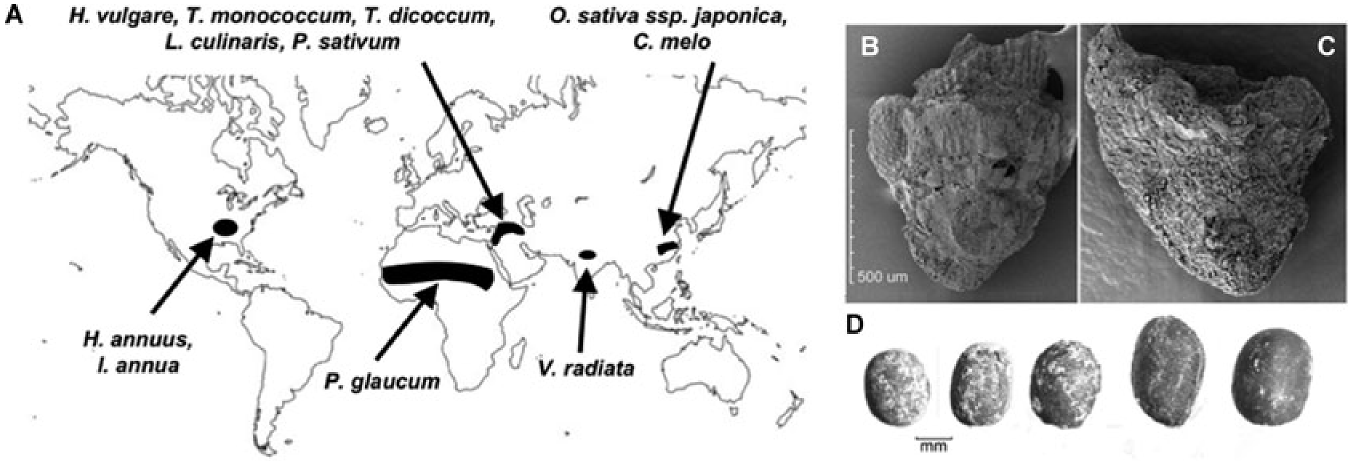

Figure 1. Archaeological sites and sample phenotypes. (A) The general region of origins of domesticated crop plants used in this study. Centers of origin are shaded black, and these are where archaeological sites used in this study are found. (B) SEM micrographs of wild and (C) domesticated spikelet bases in rice from the Tianluoshan site, ~6700 BP. The wild rice spikelet is characterized by a clean abscission layer at the base. (D) Grain size increase in *V. radiata* (mung bean) in archaeological sites in India. The first three seeds (left) are from the Neolithic (between 3700 to 3400 BP). The second to the right is an example from the Late Neolithic (~3200 BP), whereas the right shows a seed example from the Early Historic (~2050 BP).

methods, such as the advent of sickle harvesting, which selects for retention of seed after harvesting. It has been suggested that selection for nonshattering can be strong, with evolutionary models in barley indicating that this trait can be fixed in <100 generations (Hillman and Davies 1990). Molecular population genetic analysis of the *sh4* gene in rice, which controls the seed shattering phenotype, concludes that a nonshattering allele could possibly have spread throughout *Oryza sativa* within 72–112 years (Zhang et al. 2009). In archaeological records, the evolution of nonshattering in cereal crops is readily identified by the remains of infructesence rachis segments or spikelet bases with nondehiscent attachment scars (Tanno and Willcox 2006; Fuller et al. 2009).

Grain or seed size is another trait readily measured in archaeological samples and widely regarded as associated with domestication (see Fig. 1). Indeed, both Darwin (1883) and De Candolle (1884) noted that increase in seed size is a key feature in plant domestication. Ecological studies demonstrate that larger seeds are selected for with deep burial conditions associated with tillage during human cultivation, and grain size increases in cereal crops generally occur in tandem with the rise of nonshattering (Harlan et al. 1973; Fuller and Allaby 2010; Fuller et al. 2010). Like seed nonshattering, it has been suggested that this trait evolves rapidly during domestication, and experimental cultivation of rice found measurable increase in average grain weight within just five generations (Oka and Morishima 1971), suggesting that grain size can evolve quickly.

To measure evolutionary rates of domestication traits, we compiled data on seed nonshattering and grain/seed size from several archaeological studies in both Eurasia and North America, encompassing 11 crop species. These include five cereal (*Hordeum vulgare, Triticum monococcum, T. dicoccum, Pennisetum glaucum* and *O. sativa*) and three legume species (*Vigna radiata, Pisum sativum, Lens culinaris*), and also data from *Cucumis melo, Helianthus annuus,* and *Iva annua*. All these are annual crop species, all but one (*C. melo*) of which were domesticated largely as seed crops.

The archaeological data from these species are from 60 sites in five regions in Asia, Africa, and North America (see Fig. 1), with archaeobotanical remains that date from the Neolithic (~12,000 years ago) to historical times (~800 years ago). We focus our analysis on the time during which domestication—defined as the process in which species become fully dependent on humans for dispersal (i.e., evolution of nonshattering in seed plants)—is thought to have occurred. We then compare our observed rates in domesticated taxa to evolutionary rates in wild species, addressing the question of whether domestication is indeed a case of rapid evolutionary diversification or has a similar tempo to cases of natural selection.

Methods

Phenotypic data from archaeological studies were obtained from the literature, either from journal articles or archaeological site monographs. We traced primary reports from recent regional reviews (e.g., Colledge et al. 2004; Fuller 2006), and found those which have appropriate quantitative data. We used data from sites that measured the traits in greater than 10 samples and if there were at least three time points available during the domestication period. If the dates for the archaeological material were reported as a range, we used the midpoint as the date in our analyses; this was often the case for North American, Indian, and Chinese data. For those data in which raw radiocarbon data were available, especially from Southwest Asia, we recalculated date calibrations and produced summed probability distributions from all the dates of a particular site or site-phase. From this 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 the Supporting information, which addresses the dating for each of the Near Eastern sites and shows the probability distribution of summed dates, and provides references on the data sources. For regions outside the Near East, this is less of a problem as we are dealing with fewer sites, fewer dates, and more recent research (since the 1980s) when radiocarbon calibration became established.

The domestication period was defined as 4000 years from the date in which archaeological studies indicate the species was first cultivated. For our purposes, we define a species as domesticated if it is dependent on humans for dispersal; in the archaeological record, it is generally agreed that the predominance of nonshattering is the clear marker for a domesticated seed crop species (Harlan 1992; Zohary and Hopf 2000; Purugganan and Fuller 2009). Our assumed domestication time period is based on studies in einkorn, barley and rice, which suggests that nonshattering is fixed over this time span (Tanno and Willcox 2006; Fuller 2007; Fuller et al. 2009). For nonshattering data, we used the first time point within this domestication period that had spikelet/rachis bases that showed evidence for nonshattering. Because we are also interested in the domestication process, we limit our analysis to data only from sites that are found within the presumed area of domestication for a given species (e.g., Fertile Crescent for barley and wheat, Lower Yangtze Valley for rice). For *P. glaucum*, however, we considered one site in India outside of its African center of origin that had material within the time-frame of pearl millet domestication. It should be noted that einkorn grain measurements from some PPNA sites (Mureybit, Jerf el Ahmar, Djade) included grains of rye (*Secale* sp.), because these are difficult to separate on morphological grounds, and these sites had chaff evidence for the presence of rye (Willcox and Fornite 1999; Willcox 2004). Nevertheless exclusion of these assemblages would make no difference to the overall trend. All the data are available in Supplemental Data, and the Supplemental Text.

Evolutionary rates in darwins is given by the equation 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. Standard errors of the slopes were also estimated. The trait value for nonshattering is the frequency of nonshattering spikelet/rachis bases.

Evolutionary rates in haldanes is given by the equation haldanes = $[(x_2 - x_1)/\sigma_p]/[t_2 - t_1]$, where x_1 and x_2 are the mean trait values at time points t_1 and t_2, respectively, in generations and σ_p is the pooled standard deviation for the trait across the time points (Gingerich 1993). Our species are all annuals, and even in historical times generally lead to one cropping season/year; we thus assume that there is one generation per year. 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 Pearson and Hartley (1976), which is multiplied by the difference of the observed maximum and minimum. In some cases, we have combined data from across several samples for a site, and calculated a weighted mean, and then derived standard deviation by the same formula based on the total number of specimens. For nonshattering, the standard deviation of the frequency of nonshattering spikelet/rachis bases is given as

$$\sigma = [nd(1 - d)/(n - 1)]^{1/2},$$

where n is the sample size and d is the frequency of nonshattering rachises/spikelets. The pooled standard deviation is given as

$$\sigma_p = \left\{\left[\sum (n_i - 1)(\sigma_i)^2\right] \Big/ \left[\sum n_i - 1\right]\right\}^{1/2},$$

where σ_i and n_i are the standard deviation and sample size for timepoint i, respectively, and we sum across all timepoints. We also fit least-squares linear models to obtain the evolutionary rate estimate, including standard errors. The selection coefficient for a trait, s, is given as haldane rate/h^2, where h^2 is the trait heritability (Kinnison and Hendry 2001).

To compare rates during domestication with wild species, we use data from plants (Bone and Farres 2001), excluding rates calculated from direct selection of traits by humans on agricultural species. We also use the data from Hendry et al. (2008) as reported in the Supplemental Information of their paper; for these data, we use only allochronic and not synchronic data. We also use the database of selection strengths reported in Kingsolver et al. (2001), as deposited in the Dryad data repository (http://hdl.handle.net/10255/dryad.166). Statistical comparison of rates between groups used the t-test on the log-transform of the estimated rates.

There are several things to note in using the archaeological record for our analyses. First, given that data for a single species may arise from archaeological sites found in various geographic locations, an underlying assumption is that material from disparate sites is 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 (Allaby et al. 2008; Feldman and Kislev 2009; Allaby 2010); given that we use data geographically limited to the domestication center of origin, we feel this is a reasonable assumption.

Second, environmental heterogeneity between sites and times will undoubtedly affect phenotypes. The effect of this is to increase the noise in the data, although our results (see below) appear to indicate that we have a reasonable ability to estimate rates as evidenced by moderate-to-high r^2 values for many of our estimates.

Third, it is possible that phenotypic plasticity to the more favorable environments of cultivated fields may be responsible for the trait phenotypes observed in archaeological material. Phenotypic plasticity is unlikely to account for the directionality of trait phenotypes over the protracted period of time that spans the domestication process, although improved cultivation techniques during this time span may contribute to the observed trend. Genetic studies, moreover, have shown that the phenotypes we study have a large genetic component (i.e., high heritabilities) (Kato 1990; Young 1991; Gu et al. 2005; Fox et al. 2006; Sadras 2007), indicating that phenotypic differences are more likely to have a strong genetic basis.

Results

NONSHATTERING IN CEREAL CROPS EVOLVES SLOWLY AND RISES TO FIXATION OVER SEVERAL THOUSAND YEARS

The nonshattering trait is readily identified in archaeological samples of cereal grass species, because shattering seed will lead to a clean abscission break in rachis or spikelet bases (see Fig. 1). We examined data from 8189 rachis/spikelet bases in 12 sites to estimate the rate of the evolution of nonshattering in *H. vulgare* (barley), *T. monococcum* (einkorn wheat), and *O. sativa* (rice) (see Supplemental Data). In contrast to previous assumptions, archaeobotanical evidence reveals that nonshattering evolves slowly in these three plant species. Einkorn wheat from Fertile Crescent Neolithic sites took >3000 years to go from ∼22% at the Tell

Table 1. Rate of evolution of nonshattering.

Species	Date of origin (BP)	Time range (BP)	Rate (darwins)	r^2	Rate×10^3 (haldanes)	r^2
H. vulgare	12,000	11,075–8350	943.8±196.9	0.77^{**}	1.3±0.2	0.81^{***}
T. monococcum	12,000	11,725–8675	532.8±159.7	0.59^{*}	0.9±0.2	0.79^{*}
O. sativa	9000	6900–6600	1159.6±283.7	0.94	0.8±0.2	0.96

Qaramel in Syria in 11,725 years before present (BP) (Tanno and Willcox 2006) to $\sim$95% in Catal Hoyuk in Turkey by 8675 BP (Kislev 1997; Fairbairn et al. 2002). Recently characterized rice at Tianluoshan in the Lower Yangtze Valley in China also documents increases in the percent of nonshattering spikelet bases from $\sim$27% to $\sim$39% in a 300-year period (6900 to 6600 years BP) that spans the middle-to-late period of domestication (Fuller et al. 2009), which suggests a fixation time span for nonshattering in rice $>$ 2500 years.

Nonshattering appears to have been fixed most rapidly in barley, increasing in Fertile Crescent Neolithic sites from less than 4% $\sim$11,075 BP in Netiv Hagdud in Israel (Kislev 1997) to $>$90% approximately 8350 BP in Wadi Fidan, El Kowm II and Catal Hoyuk sites throughout the Fertile Crescent (De Moulins 1997; Colledge 2001; Fairbairn et al. 2002). These data indicate that nonshattering (and thus domestication) did not occur rapidly, but may have taken several thousand years to rise to fixation in these cultivated cereal crop species.

We estimated rates of the evolution of nonshattering based on a linear least-squares regression model of the archaeological trait data for these three cereal grass species (see Table 1, and Fig. 2 and Supplemental Figures). In general, the fit of the data is good, with r^2 values of $\sim$0.6 to $>$0.9, and for barley and einkorn wheat this correlation was significant. Rice had the highest coefficient of determination ($r^2 = 0.94$), but this was nonsignificant due to the small number of timepoints ($n = 3$) in the dataset.

The estimated rates in darwins are correlated with the time to fixation of the trait, with high rates for both barley ($\sim$944 ± 197 darwins) and rice ($\sim$1160 ± 284 darwins), and with einkorn wheat evolving more slowly, about half as fast ($\sim$533 ± 160 darwins, see Table 1). Relative to the standard deviation in trait values, however, it appears that all three cereal crop species have similar evolutionary rates ($0.8–1.3 \times 10^{-3}$ haldanes, see Table 1).

In archaeological data for barley, several spikelet bases could not be classified and were described as indeterminate. In our analysis, we ignored these indeterminate bases, but we also calculated

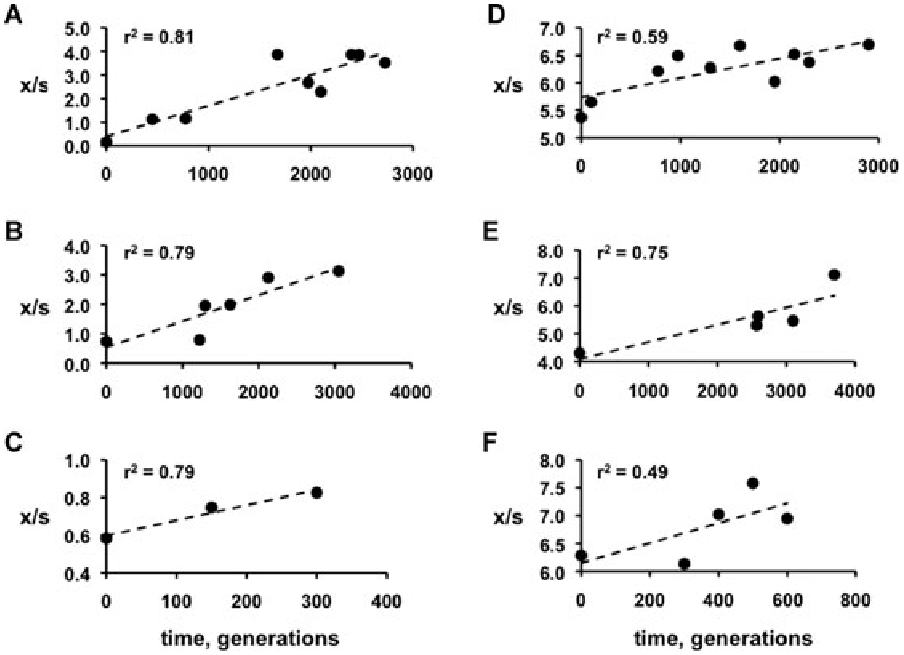

Figure 2. Estimation of evolutionary rates of nonshattering and grain/seed size evolution. Representative plots are for trait values/standard deviation with time in generations for seed nonshattering in (A) barley, (B) einkorn wheat, and (C) rice, and seed size increase for (E) thickness in emmer wheat, (F) width in sunflower, and (G) melon seeds. The dashed lines are the least-squares linear regression of the data, with the fit (r^2) indicated in each plot. The slope of the fit line equals to estimate for evolutionary rate in haldanes.

evolutionary rates assuming that they represented either wild or domesticated phenotypes. The rate estimates (rate $\sim$990 darwins if indeterminate classed as wild, and rate $\sim$786 darwins if indeterminate classed as domesticated) are fairly similar to the calculated evolutionary rate if we ignore the indeterminate spikelet bases, and does not impact our conclusions.

THE EVOLUTION OF SEED SIZE DURING DOMESTICATION

We used size measurements on 10,516 grains/seeds from 54 archaeological sites for 11 cereal, legume and other species to estimate rates of evolution for grain/seed size increase (see Supplemental Data). Grains or seeds generally appear in the archaeobotanical record as carbonized material resulting from fire exposure, leading to a shrinkage of 10–20% and some distortion in shape (see, e.g., Zohary and Hopf 2000; Willcox 2004; Braadbart and Wright 2007); it is generally assumed, however, that this affects all carbonized material similarly from different sites.

Wheat and barley grains begin to show increases in size from the Pre-Pottery Neolithic (PPN) A and early PPNB approximately 11,100–10,500 BP, as observed in Jerf el Ahmar in Syria (Willcox 2004) and ZAD-2 in Jordon (Meadows 2004). Other species, however, such as *P. glaucum* and *V. radiata* (Fuller 2007) show increases in grain size later in the domestication period. Like the nonshattering analysis, the fit of the data is generally good (see Table 2, and Fig. 2 and Supplemental Figures), with nine 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 $\sim$50 to 350 darwins and $0.3 – 2.3 \times 10^{-3}$ haldanes (see Table 2).

The exception to these rates appears to be peas, which show very slow rates of evolution (rate = 13.6 darwins or 5×10^{-5} haldanes), with a poor fit to the data ($r^2 = 0.00$–0.03). Indeed, regression estimates of evolutionary rates for legume species in general show a poorer fit to the data, with lower r^2 and higher relative standard errors for the rate estimates. Examining the data for this group, we observe an interesting pattern of an apparent earlier rapid increase in seed size followed by a general plateau in size enlargement (unpublished observations). We recalculated the evolutionary rates for legume species assuming a domestication period of 2000 years and not 4000 years (see Fig. 3 and Table 3). Under this assumption, evolutionary rate estimates for seed size increase by $\sim$5- to $\sim$60-fold (although the latter is for *P. sativum*,

Table 2. Rate of evolution of grain/seed size.

Species	Trait	Date of origin (BP)	Time range (BP)	Rate (darwins)	r^2	Rate$\times10^3$ (haldanes)	r^2
Cereals							
H. vulgare	breadth	12,000	11,400–8100	125.7±22.9	0.77***	1.0±0.2	0.77***
H. vulgare	thickness	12,000	11,400–8100	152.9±36.5	0.69**	1.2±0.3	0.68**
T. monococcum	length	12,000	11,725–8250	128.7±31.6	0.65**	0.8±0.2	0.62**
T. monococcum	breadth	12,000	11,725–8250	169.3±20.7	0.88***	1.2±0.1	0.89***
T. dicoccum	breadth	11,500	10,400–7500	36.5±20.8	0.28	0.3±0.2	0.29
T. dicoccum	thickness	11,500	10,400–7500	58.3±17.2	0.59**	0.4±0.1	0.59**
O. sativa	breadth	9000	7800–5200	71.6±16.9	0.54***	0.5±0.1	0.54***
O. sativa	breadth	9000	7190–5200	45.0±34.5	0.12	0.3±0.2	0.13
P. glaucum[1]	breadth	4500	3750–1400	123.1±97.5	0.28	0.6±0.5	0.25
P. glaucum[1]	thickness	4500	3750–1550	235.7±92.3	0.77	n.a.	n.a.
Legumes							
L. culinaris	length	11,500	11,400–7700	57.3±25.2	0.28	0.4±0.2	0.26
V. radiata	length	4500	3650–2200	186.6±196.5	0.18	1.6±1.6	0.19
V. radiata	breadth	4500	3650–2200	171.0±183.8	0.18	1.6±1.8	0.16
P. sativum	length	11,500	11,400–8000	13.6±29.1	0.03	0.05±0.3	0.00
Others							
I. annua	length	5000(?)	5400–1600[2]	154.4±33.6	0.95	1.0±0.1	0.98*
H. annus	breadth	5000(?)	4500–800	114.6±31.2	0.82*	0.6±0.2	0.75*
C. melo	length	4500	4500–3900	265.2±154.4	0.50	1.8±1.0	0.49
C. melo	width	4500	4500–3900	376.8±207.6	0.52	2.3±1.3	0.52

[1] One site in India was included in the analysis.

[2] Time point slightly earlier than the presumed start of domestication was included in the analysis.

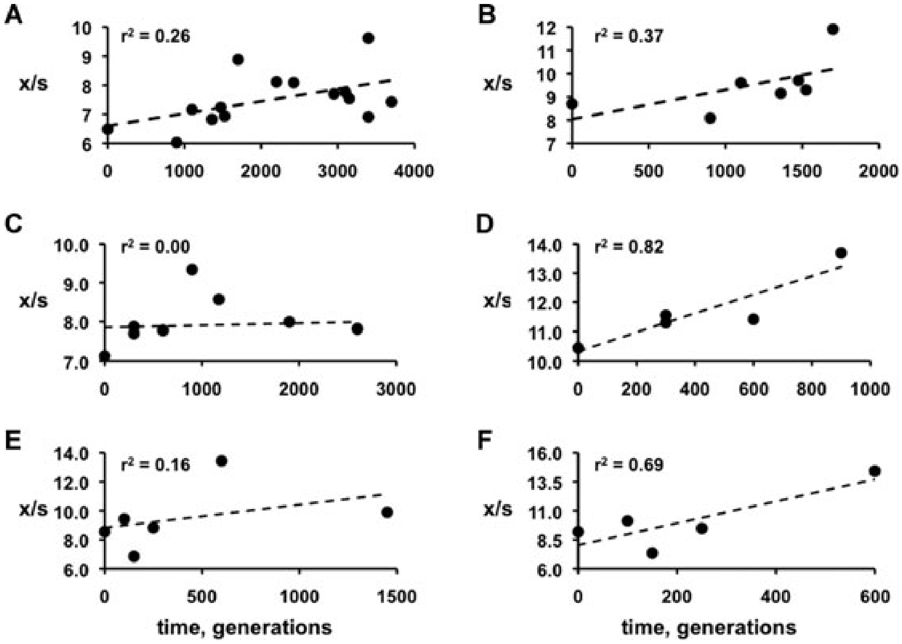

Figure 3. **Estimation of evolutionary rates of grain/seed size evolution in legumes. Plots are for trait values/standard deviation with time in generations for seed nonshattering in legume species. The left column shows plots using the standard estimate of the domestication period of 4000 years from the start of domestication, whereas the right is for a shortened period of 2000 years. (A)–(B) *L. culinaris* length, (C)–(D) *P. sativum* length, and (E)–(F) *V. radiata* breadth. The dashed lines are the least-squares linear regression of the data, with the fit (r^2) indicated in each plot. The slope of the fit line equals to estimate for evolutionary rate in haldanes.**

which shows a poor fit to the data at the longer domestication period). There is no independent evidence to assume a shorter domestication period for legumes, but we use both estimates separately in subsequent statistical analyses (see below).

COMPARISON OF RATES FOR NONSHATTERING VERSUS GRAIN/SEED SIZE INCREASE

In general, absolute rates of evolution for seed size increase are lower than the rate of nonshattering evolution. In the three cereal grasses for which we have data on both traits (*H. vulgare, T. monococcum,* and *O. sativa*), rates of evolution of nonshattering as estimated using darwins is ~3- to 20-fold higher than rates for grain size increase. We tested for significance of this rate difference with a log-transformation to normalize the rate distribution. Across all the data, the mean evolutionary rates using the log-transformed data for nonshattering is 835.4 ± 196.1 darwins, whereas for grain/seed size increase it is 107.5 ± 20.7 darwins. Using the log (rate) estimates, we find that the evolutionary rates are significantly different ($t = 4.23$, df = 19, $P < 0.0005$). Even if we assume a higher rate for legume seed size increase (mean = 150.4 ± 29.9 darwins), the difference is significant ($t = 3.25$, df = 19, $P < 0.0042$). This is perhaps to be expected because seed size is controlled by multiple genes, while individual loci may have a strong affect on shattering/nonshattering (Fuller and Allaby 2010).

The differences in scale between various traits, however, may explain the comparatively lower rate of evolution for grain/seed size increase compared to nonshattering. The possibility that trait scale differences may underlie this observation is supported by the analysis of evolutionary rates normalized with the standard deviation (haldanes, see Table 2). Across all the data, the mean evolutionary rate for nonshattering is $0.98 \pm 0.14 \times 10^{-3}$ haldanes,

Table 3. **Alternate estimates of evolutionary rates for legumes.**

Species	Trait	Date of origin (BP)	Time range (BP)	Rate (darwins)	r^2	Rate$\times 10^3$ (haldanes)	r^2
L. culinaris	length	11,500	11,400–9700	129.2±73.6	0.38	1.3±0.7	0.37
V. radiata	length	4500	3650–3050	729.5±491.3	0.42	8.3±4.4	0.54
V. radiata	breadth	4500	3650–3050	827.4±379.3	0.61	9.5±3.6	0.69*
P. sativum	length	11,500	11,400–9700	133.8±45.1	0.69*	3.2±0.9	0.82*

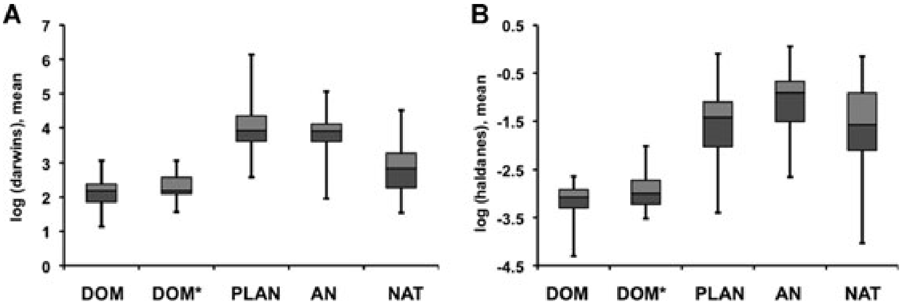

Figure 4. Comparison of evolutionary rate estimates. Box plots of the rates of evolution in (A) log (darwins) and (B) log (haldanes) for domestication (DOM) as well as plants (PLAN) (from Bones and Farres 2001) and anthropogenic (AN) and natural (NAT) conditions for wild animal species (Hendry et al. 2008). The asterisk indicates domestication rates under the assumption of the shortened 2000-year period for legume species. The vertical lines give the estimate ranges, whereas the boxes span the minimum and maximum quartile range. The horizontal line within the box gives the median rate.

while for grain/seed increase is $0.68 \pm 0.15 \times 10^{-3}$ haldanes. Using the log (rate) estimates, we find that the evolutionary rates are not significantly different ($t = 0.63$, df = 18, $P < 0.54$). In contrast, however, making the assumption of an ~2000-year domestication period for legumes leads to a nearly twofold higher estimate for grain/seed size increase across all species (mean = $1.15 \times 10^{-3} \pm 0.26$ haldanes), but this rate difference between nonshattering and seed size increase is still not significant ($t = 0.34$, df = 18, $P < 0.74$). This analysis does not reveal a significantly higher rate for nonshattering compared to grain size evolution.

EVOLUTIONARY RATES DURING DOMESTICATION ARE SIMILAR TO THOSE EXPERIENCED BY WILD SPECIES

The real interest in calculating evolutionary rates for these different domestication traits lies in the comparison with estimates observed in wild species that are subject to natural selection. There have been extensive compilations of phenotypic rates of evolution from contemporary microevolutionary (Hendry and Kinnison 1999; Bone and Farres 2001; Kinnison and Hendry 2001; Hendry et al. 2008) and paleontological data (Gingerich 2001), and we can use these to compare domesticated versus wild species.

The rate estimates for evolution during domestication fall within the range observed in these microevolutionary studies, but on the lower side of the range, either those for plants (Bone and Farres 2001) or under natural and anthropogenic conditions in animals (Hendry et al. 2008,) see Figure 4. Comparison with the plant data (Bone and Farres 2001), for example, reveals that the mean rates of evolution based on log-transformed data are much higher than those observed for the rate of evolution during domestication (see Fig. 4 and Table 4). Indeed, the mean evolutionary rates we observe during domestication are significantly lower than mean rates of phenotypic evolution of plant species in the wild ($t = 7.48$, df = 91, $P < 0.0001$).

Most of the studies that document rapid evolution in wild plant species, however, represent cases of very strong selection (e.g., growth in serpentine soils, herbicide resistance, Bone and Farres 2001). To examine evolution of other wild species, we also compare our results to data from wild animal species (Hendry et al. 2008). Moreover, the large size of the dataset (Hendry et al. 2008) allows us to focus on allochronic data (e.g., change across a time series, which is comparable to the our archaeological data), and to partition the data for wild species into those that have experienced natural versus anthropogenic conditions. This comparison is based on the assumption that, in contrast to the compiled data from plants under strong selection pressures (Bone and Farres 2001), the rates of evolution under less-stringent selective conditions are at least broadly comparable between plants and animals.

Not surprisingly, the mean rates of evolution for wild species under anthropogenic conditions are higher than those under natural conditions (see Fig. 4 and Table 4). Nevertheless, the mean rate of evolution under domestication is significantly lower than

Table 4. Mean rates of evolution.

Mean Rates	Rate (darwins)	Rate $\times 10^3$ (haldanes)
Domestication		
Overall	144.56±33.55	0.73±0.14
Overall[1]	200.82±44.04	1.17±0.26
Nonshattering	835.44±196.13	0.98±0.16
Grain/seed size	107.92±20.7	0.69±0.16
Grain/seed size[1]	158.35±32.15	1.21±0.29
Natural		
Plant	8893.8±2604.8	33.4±10.5
Anthropogenic animal	5906.7±781	71.3±18.4
Natural animal	626.2±86.4	29.5±5.4

[1] Rates calculated under the assumption that legume domestication occurred over a 2000-year period.

those under anthropogenic conditions in the wild, either when considering darwins ($t = 11.21$, df $= 140$, $P < 0.0001$) or haldanes ($t = 12.44$, df $= 53$, $P < 0.0001$). Domestication rates are even significantly lower compared to evolution of natural species in the wild ($t = 3.88$, df $= 169$, $P < 0.0002$ for darwins; $t = 8.77$, df $= 122$, $P < 0.0001$ for haldanes). The differences in overall rates for domestication are also significantly lower even if we take into account a higher evolutionary rate for seed size in legumes ($t = 3.02$, df $= 169$, $P < 0.003$ for darwins and $t = 7.61$, df $= 122$, $P < 0.0001$ for haldanes, see Table 4).

The mean rates of evolution can also be examined separately for nonshattering and seed size increase (see Table 4). It is clear that even considering these two traits separately, the rates of evolution under domestication remains lower than those for species in the wild. The one exception is between nonshattering and traits under natural conditions for animals (see Table 4), for which the absolute rates of evolution (darwins) are comparable and not significantly different ($P < 0.77$).

TIME DEPENDENCE OF RATE ESTIMATES

One consideration in evolutionary rate studies is the sensitivity of rate estimates to the timescale of analysis, and it has been shown that rates are negatively correlated with time (Gingerich 1983; Roopnarine 2003). Unlike the timescale of contemporary microevolutionary studies, archaeological data of domesticated plant species are higher (~300–3500 years), which would bias rate estimates downwards. If the rate is variable through time, then our rate estimates represent the mean rate over the domestication period, because reversals or periods of stasis are averaged with periods of stronger directional evolution. Evolution over shorter timescales may have been much stronger if it were variable in direction over time.

We can take this time dependence into account in two ways. First, we plot our observed rate estimates against timescale and extrapolate to contemporary microevolutionary timescales, as has been done in other studies (Gingerich 1983, 2001). There is a significant negative correlation of estimated rates with time in our data for both darwins ($r^2 = 0.21$, $P < 0.04$) and haldanes ($r^2 = 0.30$, $P < 0.017$, see Fig. 5). Taking into account this time dependence, the estimated evolutionary rates during domestication for our traits are 559.12 darwins and 1.66×10^{-3} haldanes at $t = 0$, which then represents the minimum mean rate of evolution over time. These estimates are still lower or equivalent to the mean rates for contemporary microevolution (see Table 4).

Second, we can compare our results from those of paleontological studies in this temporal range. We have been unable to obtain compiled data from previously published analyses of paleontological studies, but it does appear from these studies that fossil species whose morphological divergence has been measured at this timescale have evolutionary rates that range from $\sim 0.03 \times 10^{-3}$ to 32×10^{-3} haldanes (Gingerich 2001). Rate estimates for fossil data at comparable time scales are thus not generally lower but span the evolutionary rates observed in the archaeological record for domesticated species.

ESTIMATING SELECTION COEFFICIENTS FOR DOMESTICATION TRAITS

Heritability estimates for domestication traits allow us to calculate selection coefficients for these traits from the haldane rates of phenotypic evolution (Kinnison and Hendry 2001). Heritability values (h^2) during domestication for these traits are unknown, but we can approximate them using genetic data from contemporary studies, and they do not appear low. For nonshattering, trait heritability has been estimated at $h^2 = 0.4$ in a cross between wild *O. rufipogon* and cultivated *O. sativa* (Gu et al. 2005), and a similar estimate was obtained for the grass *Panicum coloratum* (Young 1991). The heritabilities of grain/seed size have been measured for barley ($h^2 > 0.88$) (Fox et al. 2006) and rice ($h^2 = 0.56 - 0.8$) (Kato 1990). Seed mass in *Helianthus, Pisum* and *Triticum*, which we can assume is highly correlated with seed size, has h^2 estimates ranging from 0.75 to 0.99 (Sadras 2007).

Using $h^2 = 0.4$ for seed nonshattering leads to an estimate of the selection coefficient, s, at $2.00–3.25 \times 10^{-3}$ for nonshattering in the three cereal crop species (see Fig. 6). In the seed

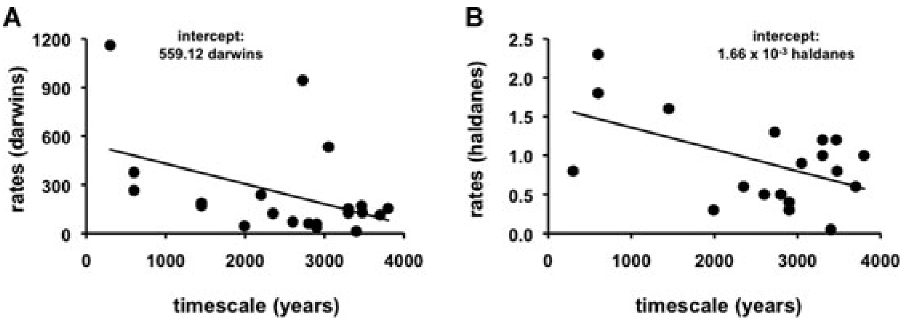

Figure 5. Time dependence of evolutionary rates for domestication traits. The least squares regression through the data for both darwins and haldanes as a function of time is shown by the solid line.

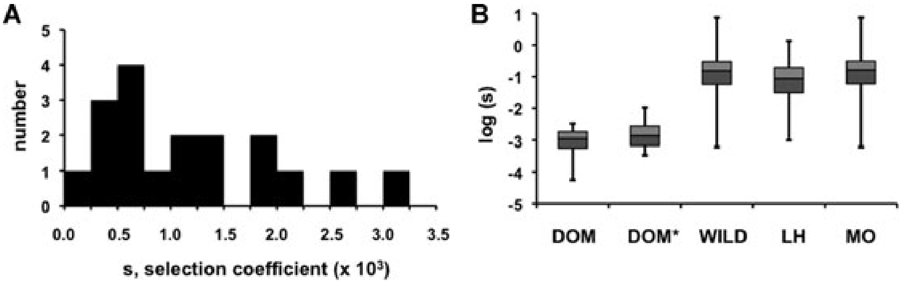

Figure 6. Distribution of selection coefficients for domestication traits. (A) The distribution is based on haldane rate estimates (given a 4000-year domestication period) under an assumptions of $h^2 = 0.4$ for nonshattering and $h^2 = 0.9$ for grain/seed size variation. (B) Box plots of selection coefficients for domestication (DOM), as well as estimates for selection in the wild (WILD) (Kingsolver et al. 2001). For the traits in the Kingsolver et al. 2001 database, we also partitioned the data into life history (LH) and morphological (MO) traits. The asterisk indicates domestication rates under the assumption of the shortened 2000-year period for legume species. The vertical lines give the estimate ranges, whereas the boxes span the minimum and maximum quartile range. The horizontal line within the box gives the median rate.

size trait, using $h^2 = 0.9$ leads to an estimate of $s = 0.3\text{–}2.6 \times 10^{-3}$ in all but one of the domesticated crop species, the exception being *P. sativum* which has s values for seed size increase of 0.06×10^{-3}.

In general, the mean rate of selection coefficients is 9.2×10^{-4}, and the distribution of selection coefficients for both traits show all have $s < 4 \times 10^{-3}$ (see Fig. 6). We compared our estimated selection coefficients to estimates from a database of standardized linear selection gradients compiled by Kingsolver et al. (2001) across all trait types ($n = 986$), as well as considering only the morphological and life-history traits that predominate in this compilation. The levels and distribution of selection in this database have been shown to be similar to those found in Kinnison and Hendry (2001). Our estimated selection coefficients for our domestication traits are largely within the range for the selection strengths measured for wild species, although it is clear that domestication is at the lower end of the distributions (see Fig. 6). The mean selection coefficient for domestication is significantly lower than those observed across all trait types in wild species, as well as either life history or morphological traits (e.g., for comparison with selection for all traits in the wild, $t = 16.47$, df $= 1004$, $P < 0.0001$). This difference between domesticated versus wild species selection strength is significant even if we consider the higher estimates of legume species associated with a 2000-year domestication period ($t = 14.86$, df $= 1004$, $P < 0.0001$). This pattern of low selection coefficients also holds even if we assume low heritabilities ($h^2 \sim 0.1$) in our domestication traits as a result of increased environmental contribution to variation, or that legume species have a shorter domestication period.

Finally, we need to caution that because we estimate haldanes over multiple generations, we actually calculate the mean selection coefficient over the domestication period. If selection is actually variable through time, then such coefficients represent the mean generational selection, because reversals or periods of stasis are averaged in with periods of stronger directional selection. If we use the haldane estimates across all traits extrapolated at $t = 0$, and assume a low heritability ($h^2 \sim 0.1$), then we arrive at a value of $s \sim 16 \times 10^{-3}$. This represents the minimum mean level of selection/generation for domestication, which is still lower than the mean rate observed for cases of natural selection in the wild reported in Kingsolver et al. (2001) (mean s in wild species ~0.12).

Discussion

Domestication has been thought to be a special case of evolutionary divergence, partly due to the influence of humans and human cultures in the origin and diversification of domesticated species. It has been suggested that selection pressures associated with domestication differs from those experienced by wild species in nature, resulting in rapid rates of evolution in crop and livestock species (Zohary 1969, 2004; Iltis 1983; Ladizinsky 1987; Hillman and Davies 1990; Innan and Kim 2004; Honne and Heun 2009; Zhang et al. 2009). This is supported by various models that posit domestication of crop species, for example, as occurring in as little as 100 years (Hillman and Davies 1990; Zhang et al. 2009). Our results, however, do not support this widespread presumption. Using allochronic data from archaeological studies on both seed nonshattering and grain/seed size increases, we find that rates of phenotypic evolution in multiple crop species appear to be significantly slower than rates observed in wild species. The tempo of phenotypic evolution in domesticated species is similar to evolutionary rates observed in paleontological data of comparable time scales.

Although we find that domestication traits evolve at significantly lower rates than traits found in species in the wild, we feel that the more pertinent observation is that the rates of evolution as well as the selection coefficients associated with domestication overlap at the lower ends of the distributions of these parameters for wild species (see Figs. 4 and 6). These findings require a reassessment of the nature of selection during domestication. There are several possible reasons for the observed slow evolutionary rates of domestication. First, it has long been appreciated, even by Darwin, that a distinction needs to be drawn between conscious human selection on desirable traits as opposed to unconscious selection that occurs during domestication, the latter arising as a byproduct of cultivating plants in agricultural environments (Darwin 1859; Heiser 1988; Zohary 2004; Purugganan and Fuller 2009). The domestication process appears driven largely by unconscious selection pressures (Heiser 1988; Zohary 2004; Fuller et al. 2010), and is in principle simply natural selection in the novel environments established by human agriculture. This is probably more true for nonshattering and grain size, traits that are not readily visible to early farmers. Moreover, at least for nonshattering, both forms are present in the crop and are so similar that the Early Neolithic farmers may have simply considered them the same crop and could not consciously differentiate cultivated from wild forms in the field (Willcox et al. 2008, 2009).

Second, genetic studies suggest that domestication genes may have pleiotropic functions (Bomblies and Doebley 2006; Vaughan et al. 2007), and that deleterious mutations may segregate at higher frequencies in the population bottlenecks associated with the origin of crop plants. These may lead to decreased selection efficiency and a slower pace of phenotypic evolution. Third, there is growing evidence that early farmers continued to cultivate and gather wild plants alongside proto-domesticates during the initial phases of domestication (Heiser 1969; Willcox et al. 2008), possibly resulting in gene flow that hampered fixation of selected alleles (Allaby 2010).

Finally, although we do observe slow rates of evolution for nonshattering and grain/seed size increase, other domestication traits not observed in the archaeological record may evolve at substantially higher levels. It should be noted, however, that the two traits we studied are very closely associated with the domestication process (Fuller 2007; Purugganan and Fuller 2009). Moreover, all of the species in our study are annual crop species, and most were domesticated largely as seed crops. We do not have data for other types of domesticated plant taxa, including tuber species and shrubs or tree species. Again, however, we feel that seed crops, which today are the most successful of domesticated plant species, provide a first glimpse into rates of evolution that may be representative of other domesticated plant taxa.

Evolutionary rates between these two domestication traits are broadly comparable, although in absolute terms nonshattering appears to evolve faster and with a higher selection coefficient than grain size increases in the three cereal crop species for which we have data for both traits. Nonshattering is the hallmark of domestication and arises from harvesting methods, such as by sickles or harvest knives, (Harlan 1992), whereas grain size increases may originate from selection for increased seedling vigor of larger grains (Harlan et al. 1973; Fuller et al. 2010). Selection associated with direct human/plant interaction (e.g., harvesting) may thus be stronger than ecological selection (e.g., seedling competition) that arises as an indirect byproduct of cultivation environments. Finally, it is noteworthy that within each domestication trait there are also comparable levels of evolutionary rates across times and locales, suggesting that selection pressures may be broadly similar even in distinct species and human cultures.

As this study demonstrates, archaeological data may prove to be a rich source of data to probe the nature of evolution during domestication. One must be clear, however, of some of the limitations of this current analysis. Archaeological data—in common with other fossil evidence—may be limited by small sample sizes at particular sites and timepoints, and experimental error in time estimates. There is also uncertainty as to whether the time period used in the rate estimates, which we assume to span the period of selection during domestication, may differ between traits and/or species. Finally, as we have noted, comparison of our evolutionary rate estimates from archaeological data to those derived from contemporary microevolutionary studies may not be appropriate. We have attempted to correct for this time dependence in rate estimates (see above), but it would clearly be better to compare the archaeological data with fossil plant data spanning similar time periods; we are not aware, however, if such data are currently available. All these and other issues highlight possible future areas of research that can fully incorporate archaeological studies in evolutionary studies.

Modeling the evolutionary history of domesticated crops (Burger et al. 2008; Zhang et al. 2009; Allaby et al. 2010) as well as identifying selected genes associated with domestication traits (Wright et al. 2005; Purugganan and Fuller 2009; Fuller and Allaby 2010), have been a clear focus of attention in studies of evolution of domesticated species. Our work suggests that these studies need to incorporate protracted times for domestication and lower selection coefficients for domestication genes than previously assumed. It also appears that plant domestication, far from being an anomalous evolutionary phenomenon, represents a valid model of evolutionary diversification in the context of human/plant mutualism, and is an example of adaptive species divergence whose dynamics are not dissimilar to those observed in wild species under the influence of nonhuman natural selection.

ACKNOWLEDGMENTS

The authors would like to thank members of the Purugganan laboratory for their critical reading of the manuscript, S. Li for help with plotting figures, and J. Banta and J. Flowers for help in some of the statistical analyses. We thank G. Willcox for providing raw metrical data from sites he has studied, and L. Qin for assistance with primary sources written in Chinese and Japanese. The authors would also like to thank the three anonymous reviewers, whose extensive input made a large impact in strengthening our article. This work was supported in part by a grant from the US National Science Foundation Plant Genome Research Program to MDP.

LITERATURE CITED

Allaby, R. G. 2010. Integrating the processes in the evolutionary system of domestication. J. Exp. Bot. 61:935–944.

Allaby, R. G., D. Q. Fuller, and T. A. Brown. 2008. The genetic expectations of a protracted model for the origins of domesticated crops. Proc. Natl. Acad. Sci. USA 105:13982–13986.

Allaby, R. G., T. A. Brown, and D. Q. Fuller. 2010. A simulation of the effect of inbreeding on crop domestication genetics with comments on the integration of archaeobotany and genetics: a reply to Honne and Heun. Veg. Hist. Archaeobot. 19:151–158.

Barker, G. 2006. The agricultural revolution in prehistory: why did foragers become farmers? Oxford Univ. Press, Oxford.

Bomblies, K., and J. F. Doebley. 2006. Pleiotropic effects of the duplicate maize *FLORICAULA/LEAFY* genes *zfl1* and *zfl2* on traits under selection during maize domestication. Genetics 172:519–531.

Bone, E., and A. Farres. 2001. Trends and rates of microevolution in plants. Genetica 112–113:165–182.

Braadbart, F., and P. J. Wright. 2007. Changes in mass and dimensions of sunflower (*Helianthus annus* L.) achenes and seeds due to carbonization. Economic Bot. 61:137–163.

Burger, J. C., M. A. Chapman, and J. M. Burke. 2008. Molecular insights into the evolution of crop plants. Am. J. Bot. 95:113–122.

Colledge, S. 2001. Plant exploitation on epipalaeolithic and early neolithic sites in the Levant. British Archaeological Reports, Archaeopress, Oxford.

Colledge, S., J. Conolly, and S. Shennan. 2004. Archaeobotanical evidence for the spread of farming in the eastern Mediterranean. Curr. Anthropol. 45:S35–S58.

Darwin, C. 1859. The origin of species. J, Murray, London.

Darwin, C. R. 1883. The variation of animals and plants under domestication. Appleton, New York.

De Candolle, A. 1884. The origin of cultivated plants. Paul and Trench, London.

De Moulins, D. 1997. Agricultural changes at Euphrates and steppe sites in the mid-8th to the 6th millennium B.C. British Archaeological Reports, Archaeopress, Oxford.

Diamond, J. 2002. Evolution, consequences and future of plant and animal domestication. Nature 418:700–707.

Fairbairn, A., E. Asouti, J. Near, and D. Martinoli. 2002. Macro-botanical evidence for plant use at Neolithic Çatalhöyük, south-central Anatolia, Turkey. Veg. Hist. Archaeobotany 11:41–54.

Feldman, M., and M. E. Kislev. 2009. Domestication of emmer wheat and evolution of free-threshing tetraploid wheat. Israel J. Plant Sci. 55:207–221.

Fox, G. P., A. Kelly, D. Poulsen, A. Inkerman, and R. Henry. 2006. Selecting for increased barley grain size. J. Cereal Sci. 43:198–208.

Fuller, D. Q. 2006. Agricultural origins and frontiers in South Asia: a working synthesis. J. World Prehistory 20:1–86.

———. 2007. Contrasting patterns in crop domestication and domestication rates: recent archaeobotanical insights from the old world. Ann. Bot. 100:903–924.

Fuller, D. Q., and R. G. Allaby. 2010. Seed dispersal and crop domestication: shattering, germination and seasonality in evolution under cultivation. Annu. Plant Rev. 38:238–295.

Fuller, D. Q., L. Qin, Y. F. Zheng, Z. J. Zhao, X. Chen, L. A. Hosoya, and G. P. Sun. 2009. The domestication process and domestication rate in rice: Spikelet bases from the Lower Yangtze. Science 323:1607–1610.

Fuller, D. Q., R. G. Allaby, and C. Stevens. 2010. Domestication as innovation: the entanglement of techniques, technology and chance in the domestication of cereal crops. World Archaeol. 42:13–28.

Gingerich, P. D. 1983. Rates of evolution—effects of time and temporal scaling. Science 222:159–161.

———. 1993. Quantification and comparison of evolutionary rates. Am. J. Sci. 293A:453–478.

———. 2001. Rates of evolution on the time scale of the evolutionary process. Genetica 112:127–144.

Grant, P. R., and B. R. Grant. 1995. Predicting microevolutionary responses to directional selection on heritable variation. Evolution 49:241–251.

Gu, X. Y., S. Kianian, G. A. Hareland, B. L. Hoffer, and M. E. Foley. 2005. Genetic analysis of adaptive syndromes interrelated with seed dormancy in weedy rice (*Oryza sativa*). Theor. Appl. Genet. 110:1108–1118.

Haldane, J. B. S. 1949. Suggestions as to quantitative measurement of rates of evolution. Evolution 3:51–53.

Harlan, J. R. 1992. Crops and ancient man. American Society for Agronomy, Madison.

Harlan, J. R., J. M. J. De Wet, and E. G. Price. 1973. Comparative evolution of cereals. Evolution 27:311–325.

Heiser, C. B. 1969. Some considerations of early plant domestication. Bioscience 19:228–231.

———. 1988. Aspects of unconscious selection and the evolution of domesticated plants. Euphytica 37:77–81.

Hendry, A. P., and M. T. Kinnison. 1999. The pace of modern life: measuring rates of contemporary microevolution. Evolution 53:1637–1653.

Hendry, A. P., T. J. Farrugia, and M. T. Kinnison. 2008. Human influences on rates of phenotypic change in wild animal populations. Mol. Ecol. 17:20–29.

Hillman, G. C., and M. S. Davies. 1990. Domestication rates in wild-type wheats and barley under primitive cultivation. Biol. J. Linn. Soc. 39:39–78.

Honne, B. I., and M. Heun. 2009. On the domestication genetics of self-fertilizing plants. Veg. Hist. Archaeobot. 18:269–272.

Iltis, H. H. 1983. From teosinte to maize: the catastrophic sexual transmutation. Science 22:886–894.

Innan, H., and Y. Kim. 2004. Pattern of polymorphism after strong artificial selection in a domestication event. Proc. Natl. Acad. Sci. USA 101:10667–10672.

Kato, J. 1990. Heritability for grain size in rice estimated from parent-offspring correlation and selection response. Jap. J. Breeding 40:313–320.

Kinnison, M. T., and A. P. Hendry. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. Genetica 112–113:145–164.

Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. Am. Nat. 157:245–261.

Kislev, M. E. 1997. Early agriculture and paleoecology of Netiv Hagdud. Pp. 203–230 *in* O. Bar-Yosef and A. Gopher, eds. An early Neolithic village in the Jordan valley. Part I: the archaeology of Netiv Hagdud. Peabody Museum of Archaeology and Ethnology, Cambridge, MA.

Ladizinsky, G. 1987. Pulse domestication before cultivation. Econ. Bot. 41:60–65.

Meadows, J. 2004. The earliest farmers? Archaeobotanical research at pre-Pottery neolithic a sites in Jordan. Pp. 119–128 *in* F. al-Khraysheh ed. Studies in the history and archaeology of Jordan VIII: archaeological and historical perspectives on society culture and identity. Department of Antiquities of Jordan, Amman.

Mueller, U. G., N. M. Gerardo, D. K. Aanen, D. L. Six, and T. R. Schultz. 2005. The evolution of agriculture in insects. Ann. Rev. Ecol. Evol. Syst. 36:563–595.

Oka, H. I., and H. Morishima. 1971. The dynamics of plant domestication: cultivation experiments with *Oryza perennis* and its hybrid with *O. sativa*. Evolution 25:356–364.

Pearson, E. S., and H. O. Hartley. 1976. Biometrika tables for statisticians. Biometrika Trust, Cambridge, UK.

Purugganan, M. D., and D. Q. Fuller. 2009. The nature of selection during plant domestication. Nature 457:843–848.

Reznick, D. N., F. H. Shaw, F. H. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 27:1934–1937.

Roopnarine, P. D. 2003. Analysis of rates of morphologic evolution. Ann. Rev. Ecol. Evol. Syst. 34:605–632.

Sadras, V. O. 2007. Evolutionary aspects of the trade-off between seed size and number in crops. Field Crops Res. 100:125–138.

Tanno, K., and G. Willcox. 2006. How fast was wild wheat domesticated? Science 311:1886.

Vaughan, D. A., E. Balazs, and J. S. Heslop-Harrison. 2007. From crop domestication to super-domestication. Ann. Bot. 100:893–901.

Willcox, G. 2004. Measuring grain size and identifying Near Eastern cereal domestication: Evidence from the Euphrates Valley J. Arcaheol. Sci. 31:145–150.

Willcox, G., and S. Fornite. 1999. Impressions of wild cereal chaff in pisé from the tenth millennium at Jerf el Ahmar and Mureybet: northern Syria. Veg. Hist. Archaeobot. 8:14–21.

Willcox, G., S. Fornite, and L. Herveux. 2008. Early Holocene cultivation before domestication in northern Syria. Veg. Hist. Archaeobot. 17:313–325.

Willcox, G., R. Buxo, and L. Herveux. 2009. Late Pleistocene and early Holocene climate and the beginnings of cultivation in northern Syria. Holocene 19:151–158.

Wright, S. I., I. V. Bi, S. G. Schroeder, M. Yamasaki, J. F. Doebley, M. D. McMullen, and B. S. Gaut. 2005. The effects of artificial selection of the maize genome. Science 308:1310–1314.

Young, B. A. 1991. Heritability of resistance to seed shattering in kleingrass. Crop Sci. 31:1156–1158.

Zeder, M. A. 2006. Central questions in the domestication of plants and animals. Evol. Anthropology 15:105–117.

Zhang, L. B., Q. Zhu, Z. Q. Wu, J. Ross-Ibarra, B. Gaut, S. Ge, and T. Sang. 2009. Selection on grain shattering genes and rates of rice domestication. New Phytol. 184:708–720.

Zohary, D. 1969. The progenitors of wheat and barley in relation to domestication and agricultural dispersal in the Old World. Pp. 44–66 *in* P. J. Ucko and Dimbleby, eds. The domestication and exploitation of plants and animals. Duckworth, London.

Zohary, D. 2004. Crop domestication - role of unconscious selection. Pp. 340–342 *in* R. M. Goodman, ed. Encyclopedia of plant and crop sciences. Marcel Dekker, New York.

Zohary, D., and M. Hopf. 2000. Domestication of plants in the Old World, 3rd ed. Oxford Univ. Press, Oxford.

Associate Editor: P. Tiffin

Supporting Information

The following supporting information is available for this article:

Figure S1. In the figures, the y-axes are ln(nonshattering frequency), and the x-axes are time in millions of years.
Figure S2. In the figures, the y-axes are x/s, where x is the trait frequency and s is the pooled standard deviation.
Figure S3. In the figures, the y-axes are ln(mean size, cm), and the x-axes are time in millions of years.
Figure S4. In the figures, the y-axes are x/s, where x is the trait mean (cm) and s is the pooled standard deviation.

Supporting Information may be found in the online version of this article.