The nature of selection during plant domestication

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Plant domestication is an outstanding example of plant–animal co-evolution and is a far richer model for studying evolution than is generally appreciated. There have been numerous studies to identify genes associated with domestication, and archaeological work has provided a clear understanding of the dynamics of human cultivation practices during the Neolithic period. Together, these have provided a better understanding of the selective pressures that accompany crop domestication, and they demonstrate that a synthesis from the twin vantage points of genetics and archaeology can expand our understanding of the nature of evolutionary selection that accompanies domestication.

Domestication is a complex evolutionary process in which human use of plant and animal species leads to morphological and physiological changes that distinguish domesticated taxa from their wild ancestors[1]. It is one of the most important technological innovations in human history and was the linchpin of the Neolithic revolution 13,000–10,000 years ago, in which groups of hunter-gatherers formed the sedentary agricultural societies that ultimately gave rise to current human cultures[2]. Domestication gave rise to food surpluses, and this led to craft specializations, art, social hierarchies, writing, urbanization and the origin of the state[2].

As a process of recent, rapid species evolution, domestication was of great interest to Charles Darwin when he formulated his thesis on the origin of species through natural selection[3,4]. Evolutionary biologists, however, tend to view domestication as a special class of species diversification, distinct from species divergence through natural selection in the wild[5]. Yet domestication can also be seen as a type of plant–animal co-evolution, conceptually similar to examples of evolutionary diversification driven by other multispecies interactions[6,7]. Indeed, the spread of crop species, which today dominate landscapes across the planet, attests to the increased fitness of domesticated plant taxa and suggests that domestication is one of the most successful of all plant–animal mutualisms. Moreover, fungal species have been domesticated by ants[8] and beetles[9], so domestication is not specific to *Homo sapiens*. Nevertheless, the role of human culture, including the intentional manipulation of plants as sources of delayed food returns, drives the domestication process in distinctive ways.

The use of domestication as a model for the evolutionary process stems from an understanding of events associated with the origins of crop species (starting some 13,000 years ago) and from precise knowledge of the selective pressures experienced by domesticated taxa, which can be gleaned from archaeological data and ethnographic studies of traditional farming societies and hunter-gatherers. Archaeology, in particular, can establish a fossil framework in which changes in phenotypes can be tracked in space and time and dated relatively precisely, allowing the microevolutionary dynamics that accompany species diversification to be traced. Genetic information on crop species also provides a molecular framework in the study of this co-evolutionary process[10,11], linking selective mechanisms inferred from archaeological studies to the genes that drove the origin and diversification of crop plant species.

In this Review, we discuss recent archaeological work that reveals the mechanisms of the adaptation of crop plants to cultivation in agricultural environments and human cultures, and we describe genetic and genomic studies into the nature of adaptive selection in the genomes of crop species. The focus on both genetic and archaeological insights provides a clear picture of the selective pressures that accompany crop origins and diversification. The view from these two vantage points can increase understanding of the nature of the evolutionary selection that accompanies plant domestication.

Cultivation and the rise of domesticated species

Humans were initially foragers and for a long time ate wild cereals, as well as seeds and nuts. Evidence from the Ohalo II archaeological site in Israel, for example, shows that wild wheat and barley were used at least 10,000 years before the advent of cultivation[12]. Beginning in the Epipalaeolithic and into the Neolithic period (13,000 to 11,000 years ago), however, foraging gave way to cultivation, representing a shift of labour investment to just a few plant species as food sources[13,14] and a change in human behavioural ecology that selected for recurrent adaptations, leading to domestication[13,15,16].

Archaeological evidence suggests that hunter-gatherer groups independently began cultivating food plants in 24 regions, and grain crops (mostly grasses) were the focus of early cultivation in perhaps 13 regions (Fig. 1). Several traits evolved that result in the distinctive morphologies and physiologies that distinguish many domesticated plant species from their wild ancestors. Domestication traits differ between plants, depending on the way they are used, for example whether they are grown for fruits and vegetative organs or edible seeds[15,16]. Changes in grain crops — including various seed traits, a shift to an annual life cycle, increased selfing rates and reduced lateral branching or tillering — are well documented and are the focus of this review.

Adaptations in cereal crops that evolve under human cultivation fall into two main types: responses that lead to successful germination with increased soil disturbance and depth of burial, and those that make harvesting easier[17,18]. Several of these adaptations may proceed from unconscious selective pressures that act in the same way as natural selection in the wild, albeit under the imposed agroecological environments of the cultivated field[13,17,18].

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Two such traits are increases in grain size and loss of seed shattering, both of which are well represented in archaeological data (Figs 2 and 3). An increase in seed size is an early adaptive response to human cultivation, and greater seed size is strongly correlated with larger seedlings in many cereal and legume species[19]. Comparative ecological studies show that larger seeds have advantages under certain kinds of competition, including deeper burial in soil[19,20]. Larger seeds are therefore likely to be selected for open environments, where bigger seedlings are advantageous given the deeper burial in soils disturbed by human tillage[13,17].

Measurable increases in grain size among barley and einkorn wheat in archaeological samples have been observed in the Jerf el Ahmar site in the Upper Euphrates in the Early Neolithic, some 500–1,000 years after the beginnings of cultivation[13]. This trait also shows relatively rapid local evolution (less than 500 years) in rye, as shown by the presence of enlarged grains at Abu Hureyra in Syria in the Late Pleistocene[21,22]. By contrast, archaeological evidence for rice suggests that changes in grain size[23] and husk phytoliths[24] were most intensive over a longer period, between 9,000 and 5,500 years ago. Archaeological data also suggest a period of grain size enlargement of one to two millennia[25] in a minor domesticated millet in Japan, *Echinochloa crusgalli* var. *utilis*.

The reduction of natural seed dispersal, which includes the loss of seed shattering, is the other key trait that is selected under cultivation[13,16,17]. Non-shattering is often regarded as the hallmark of domestication in most seed crops because it renders a plant species primarily dependent on humans for survival and propagation. The loss of shattering in cereal crop species generally arises from the absence of an abscission layer at the spikelet base[26] (Fig. 3) and has been attributed to the early use of sickle tools that select for the retention of seed on the plant after harvesting[27,28]. Three genes favouring seeds that do not shatter have been isolated: the rice gene *sh4* (ref. 26), which is similar to the genes encoding MYB-like transcription factors in maize; the rice quantitative trait locus (QTL) *qSH1*, which encodes a homeobox-containing protein[29]; and the wheat gene *Q*, which is similar to genes of the *AP2* family in other plants[30].

The archaeological record provides evidence that seed size enlargement can occur before the loss of shattering. In wheat and barley, archaeological studies demonstrate that an increase in grain size was followed by the fixation of non-shattering rachises[13]. There is also evidence from China that increased grain size was being selected under cultivation about 8,000 years ago[23,31], before there was a general increase in the frequency of spikelet types associated with loss of shattering. These findings indicate that seed size enlargement arises during the early history of cultivation but before the completion of plant domestication, and that an increase in grain size may be one of the first traits to experience selective pressures associated with human cultivation.

This evolutionary sequence of seed size increase before the rise of non-shattering is by no means universal, however. Grain size enlargement in pearl millet, for example, did not occur until 2,000 years after domestication[12], although evidence from Libya and India indicates that selection for grain enlargement in pearl millet occurred several times[13]. Data from India and sub-Saharan Africa also suggest that the increase in seed size in pulses was delayed by millennia after the beginning of cultivation and may not have been part of the initial domestication[32,33].

The evolution of non-shattering was also a slow process, despite modelling studies demonstrating that it can evolve in less than 100 years with the use of sickle tools[28,34]. Archaeobotanical remains of wheat and barley ears indicate that the fixation of non-shattering rachises took about 2,000 years[13,35] (Fig. 4). Recent efforts to recover rice spikelet bases, which preserve evidence for the non-shattering, domesticated, type, also show that fixation of this trait was surprisingly late in China. As recent as 7,500 to 6,500 years ago, only around half of the rice from the Lower Yangtze had the domesticated, non-shattering, morphology, and

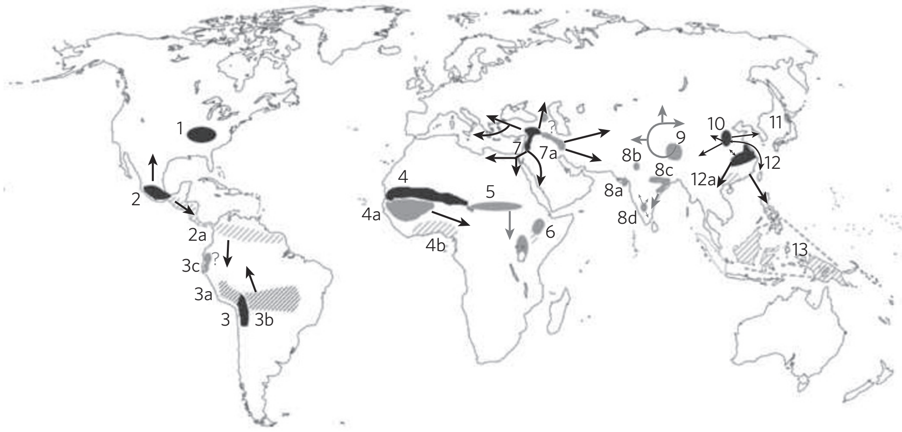

Figure 1 | Centres of plant domestication. Solid-shaded areas and hatched areas indicate regions of important seed-crop domestication and vegecultural crops, respectively. Accepted primary domestication centres are shown in black, and potentially important secondary domestication centres are shown in grey. Arrows indicate major trajectories of spread of agriculture and crops out of some centres. Areas are numbered, and examples of crop species and the year by which they were domesticated in each area are as follows: 1, eastern North America (*Chenopodium berlandieri*, *Iva annua* and *Helianthus annuus*, 4,500–4,000 years before present (yr BP)); 2, Mesoamerica (*Cucurbita pepo*, 10,000 yr BP; *Zea mays*, 9,000–7,000 yr BP); 2a, northern lowland neotropics (*Cucurbita moschata*, *Ipomoea batatas*, *Phaseolus vulgaris*, tree crops, 9,000–8,000 yr BP); 3, central mid-altitude Andes (*Chenopodium quinoa*, *Amaranthus caudatus*, 5,000 yr BP); 3a, north and central Andes, mid-altitude and high altitude (*Solanum tuberosum*, *Oxalis tuberosa*, *Chenopodium pallidicaule*, 8,000 yr BP); 3b, lowland southern Amazonia (*Manihot esculenta*, *Arachis hypogaea*, 8,000 yr BP); 3c, Ecuador and northwest Peru (*Phaseolus lunatus*, *Canavalia plagiosperma*, *Cucurbita ecuadorensis*, 10,000 yr BP; the question mark indicates that there is some question of the independence of crop origins of this centre from 3, 3a and 3b); 4, West African sub-Sahara (*Pennisetum glaucum*, 4,500 yr BP); 4a, West African savanna and woodlands (*Vigna unguiculata*, 3,700 yr BP; *Digitaria exilis*, *Oryza glaberrima*, <3,000 yr BP); 4b, West African rainforests (*Dioscorea rotundata*, *Elaeis guineensis*, poorly documented); 5, east Sudanic Africa (*Sorghum bicolor*, >4,000 yr BP?); 6, East African uplands (*Eragrostis tef*, *Eleusine coracana*, 4,000 yr BP?) and lowland vegeculture (*Dioscorea cayenensis*, *Ensete ventricosum*, poorly documented); 7, Near East (*Hordeum vulgare*, *Triticum* spp., *Lens culinaris*, *Pisum sativum*, *Cicer arietinum*, *Vicia faba*, 13,000–10,000 yr BP); 7a, eastern fertile crescent (additional *Hordeum vulgare* and, 9,000 yr BP, also goats); 8a, Gujarat, India (*Panicum sumatrense*, *Vigna mungo*, 5,000 yr BP?); 8b, Upper Indus (*Panicum sumatrense*, *Vigna radiata*, *Vigna aconitifolia*, 5,000 yr BP); 8c, Ganges (*Oryza sativa* subsp. *indica*, 8,500–4,500 yr BP); 8d, southern India (*Brachiaria ramosa*, *Vigna radiata*, *Macrotyloma uniflorum*, 5,000–4,000 yr BP); 9, eastern Himalayas and Yunnan uplands (*Fagopyrum esculentum*, 5,000 yr BP?); 10, northern China (*Setaria italica*, *Panicum miliaceum*, 8,000 yr BP; *Glycine max*, 4,500 yr BP?); 11, southern Hokkaido, Japan (*Echinochloa crusgalli*, 4,500 yr BP); 12, Yangtze, China (*Oryza sativa* subsp. *japonica*, 9,000–6,000 yr BP); 12a, southern China (*Colocasia*, *Coix lachryma-jobi*, poorly documented, 4,500 yr BP?); 13, New Guinea and Wallacea (*Colocasia esculenta*, *Dioscorea esculenta*, *Musa acuminata*, 7,000 yr BP).

there is evidence of only a gradual rise in frequency (ref. 36, and D.Q.F., L. Qin, Y. Zheng, Z. Zhao, X. Chen, L. Hosoya and G. Sun, unpublished observations) (Fig. 4).

The rate of increase of the non-shattering, domesticated, form of barley, einkorn wheat and rice can be estimated from the archaeological record and reflects the strength of selection on this trait (Fig. 4). Remarkably, these different crop species have similar rates of phenotypic selection, with non-shattering forms increasing at a rate of 0.03–0.04% per year. This suggests that selection on the loss of seed shattering in cereal crop species, and hence on domesticated morphologies, is similar across different taxa, geographical origins and time periods. The slow rate of evolution of this trait also implies weak selective pressures[13], especially compared with the relatively rapid rates of grain size evolution. The slow rise in non-shattering has been attributed to continued gene flow into proto-domesticates as humans continued to gather wild grain[37], leading to a period of metastable equilibrium in which adaptive diversity for harvesting and natural shattering coexisted in early crop populations.

From these and other archaeological data, it is clear that the origins of domesticated plant species were not single events but an extended multi-stage process in which traits arose sequentially over several thousand years to create the phenotypic assemblage that characterizes domesticated species today. The archaeological results are in contrast to molecular evolutionary studies, which have invariably assumed rapid, single origins for domestic species[38–40], when in reality these taxa may have evolved in a stepwise manner over several millennia.

Cultural and ecological adaptation

Selection after domestication has led to the immense diversity in varieties that characterizes many domesticated plant species, which, as Darwin pointed out, can exceed the range of phenotypic variation in their wild ancestors[6]. Selection for crop diversification leads to local adaptation, driven by human groups developing varieties with preferred cooking or processing qualities, the ability to grow in new environments, or desirable visual or gustatory features. Unlike domestication traits, however, selection for crop diversification may involve a greater level of conscious selection, as human cultures deliberately chose varieties with the desired characteristics.

One result of such cultural selective pressure is the development of crops that are less labour intensive to process after harvesting. In some species, this selective pressure was not local but species-wide; evolution in maize, for example, turned the hard podcase of teosinte into easily milled, but still glumed, pod-corns and then into naked-grained cobs[41,42]. This trait is controlled in part by the domestication gene *teosinte glume architecture* (*tga1*), which encodes a transcriptional activator belonging to the SBP family[42,43]. In other species, however, such as wheat and barley, local selection has resulted in diverse varieties. Recurrent evolution resulted in free-threshing sorghum races in northeast, west and southern Africa and India[44,45], and molecular data indicate that free-threshing tetraploid and hexaploid wheats evolved from ancestral glume wheats at least twice[46,47]. Archaeobotanical evidence also reveals that both tetraploid and hexaploid free-threshing wheats were present, although rare, during the later pre-pottery Neolithic in Syria and Turkey by 9,500 years ago[18,48]. Despite selective pressure for free-threshing varieties, some cultures still have a preference for hulled varieties, perhaps for improved storability or more reliable germination. As a result, hexaploid glume wheats evolved from free-threshing hexaploid wheats several times in various regions of western Eurasia[18,49].

Similarly, naked barley evolved a reduction in the tight-fitting hull and was also present in the pre-pottery Neolithic Near East[18,48]. Prehistoric Europe also had regionally varied patterns of reliance on naked barleys with six-rowed spikelets of grain[48]. Nevertheless, some cultures and periods have shown a clear preference for hulled barley, including 3,000 years ago during the Late Bronze Age in parts of northern and western Europe[50], where it may be associated with new forms of cooking or beer brewing.

Cultural selection associated with distinct food preferences is also fairly common, and this includes maize and sorghum varieties that have evolved tough pericarps and are used for making popcorn[51] and the evolution of the distinct fragrance of basmati and jasmine rice[52]. In the latter case, an increase in the levels of 2-acetyl-1-pyrroline results in part from a non-functional allele of *sk2*, which encodes a betaine aldehyde dehydrogenase, producing the distinctive aroma prized by south Asian, Thai and Iranian cultures[52].

One of the best-studied examples of post-domestication selection involves the preference for sticky cooked cereals in east Asian cultures, a property that arises from a reduction in amylose levels in grain starch. Eight cereal species in China, Korea, Japan and northern Southeast Asia are known to have sticky glutinous varieties[53], and this cultural taste may have its origins in hunter-gatherers processing starchy nuts

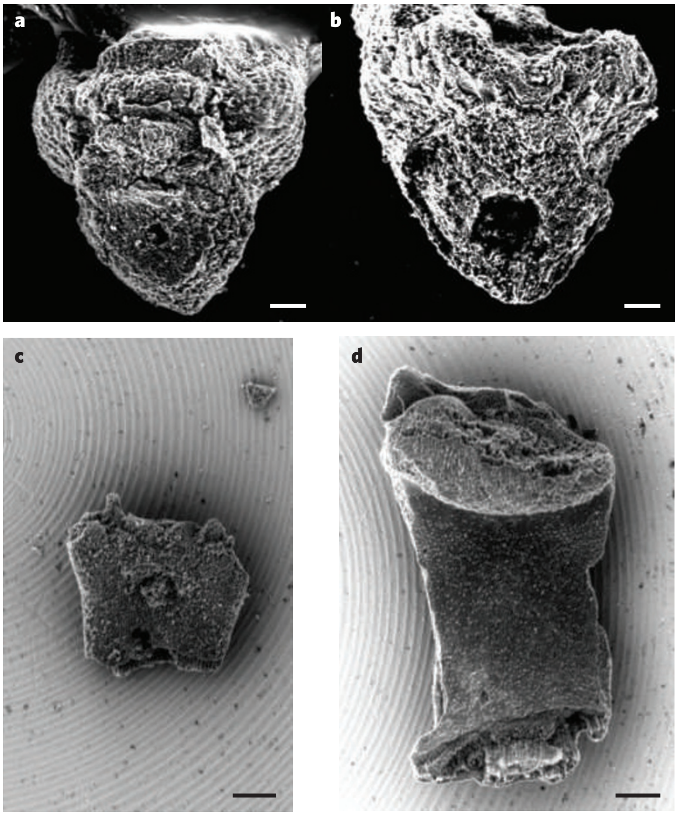

Figure 3 | The evolution of non-shattering seeds in the archaeological record. a, b, Scanning electron micrographs of charred wild (**a**) and domesticated (**b**) rice spikelet bases from the Tian Luo Shan site in China, ~6,700 yr BP. Scale bars, 100 μm. **c,** Wild-type barley rachis with abscission scar from Dhra, Jordan, ~11,000 yr BP. Scale bar, 250 μm. **d,** Typical carbonized rachis of domesticated barley with protruding rachis attachment at the top, from Kawa, Sudan, ~2,500 yr BP. Scale bar, 250 μm. (Panel **c** courtesy of S. Colledge, University College London, UK.)

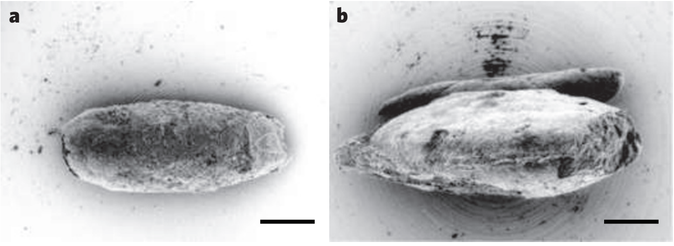

Figure 2 | Evolution of grain-size increases in the archaeological record. Scanning electron micrographs of the dorsal view of wild (**a**) and domesticated (**b**) einkorn wheat from Abu Hureyra. The wild einkorn wheat is from the pre-pottery Neolithic B (~9,300 yr BP), whereas the domesticated einkorn is from the latest levels of the site, some 8,000 yr BP or later. Scale bars, 1 mm.

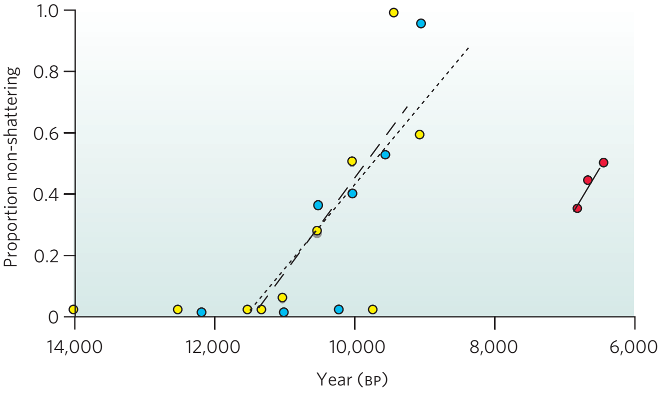

Figure 4 | Frequency of non-shattering, domesticated, forms of barley, wheat and rice in the archaeological record. The barley and wheat data are from Near Eastern sites[13], and the rice data are from the Lower Yangtze (D.Q.F., L. Qin, Y. Zheng, Z. Zhao, X. Chen, L. Hosoya and G. Sun, unpublished observations). The wheat data do not include the Kosak Shimali site[35], as it represents a later date and has a high proportion of indeterminate (damaged) rachises. The rate of increase in frequency is calculated from a linear model, with R^2 values of 0.48 for barley (yellow, long-dashed line), 0.66 for wheat (blue, short-dashed line) and 0.85 for rice (red, solid line).

and tubers[54]. The most widespread of these cereals is glutinous rice; this results from an intron 1 splice-donor mutation at the *waxy* gene, which encodes a starch-granule-bound starch synthase[55–57]. This *waxy* splice-donor mutation originated once in domesticated tropical *japonica* rice, probably in Southeast Asia[56]. By contrast, recent work on the *waxy* locus of foxtail millet has found three distinct mutations with differing geographical distributions that all produce sticky millets[58]. This parallel evolution reinforces the possibility of evolutionary genetic constraint and independent selection acting multiple times at similar loci during evolutionary diversification.

Crop species also underwent range expansions after domestication, through a combination of human migrations and the adoption of crops obtained by trade, which in many cases spread domesticated plants far from their centres of origin. Climatic and other ecological constraints control the rates and extents of domesticated migrations, as illustrated by the case of early Near Eastern crops such as wheat, barley, lentils, peas and chickpeas. These crops had spread rapidly east as far as Pakistan[59] and west through Greece by about 9,000 years ago, had reached the Balkans 8,000 years ago, and approximately 500 years later had spread to Italy, Spain and Portugal[48]. North of the Balkans and through the Carpathian Mountains, however, species spread was delayed by about 1,000 years, a pause attributed to the need to evolve either a vernalization response to cope with cold winters or photoperiod-neutral varieties that could be grown in summer[60,61]. The evolution of wheat and barley varieties that could expand to these northern latitudes allowed their spread, but species such as lentils and chickpeas did not adapt[62]. Similarly, widespread use of wheat and barley in mountainous Kashmir and northern Pakistan began about 5,000 years ago, three millennia after they arrived in the neighbouring Indus valley[59].

The nature of selection in crop genomes

Early QTL mapping studies suggest that many traits affected by domestication and diversification are controlled by just a few genes, some of which have large effects[63], although in sunflowers small-to-moderate effects are more common[64]. Comparative QTL mapping suggests that selection may sometimes have acted on the same loci several times, but in other cases different genes have been affected, for example in selection for non-shattering mutations in maize, rice and wheat[65]. Nevertheless, analysis of QTLs for disparate domestication traits reveals that selection need act on only a few genomic regions to achieve domestication, as indicated by studies in rice[66] and wheat[67]. Recent population-genomics studies, however, provide a contrasting view. The number of genes associated with crop domestication and diversification in maize, for example, is large, with 2–4% of genes in the genome showing evidence of selection[38]. Furthermore, a recent study of genome-wide nucleotide polymorphism in rice suggests that domestication may have affected the entire genome, possibly because selection acted on a large number of loci[39].

Recent successes in the isolation of genes underlying crop domestication and diversification have improved the ability to examine the genetic basis of the evolution of domesticated species. Molecular genetic studies have so far identified 9 domestication genes in plants, as well as 26 other loci known to underlie crop diversity associated with human cultural preferences or different agricultural environments[10,53,68,69]. Of the nine domestication loci, eight encode transcriptional activators[10], including the rice *shattering* genes *sh4* (ref. 26) and *qSH1* (ref. 29), maize *tb1* (which is involved in plant architecture)[70], and the *AP2*-like wheat gene *Q* (which is involved in inflorescence structure)[30]. Of the crop-diversification genes whose molecular functions are known, however, more than half encode enzymes[10,53,68,69]. Domestication, then, seems to be associated with changes in transcriptional regulatory networks, whereas crop diversification involves a larger proportion of enzyme-encoding loci. Moreover, both regulatory promoter changes and amino-acid changes (or disrupted coding sequences) are responsible for relevant evolved phenotypes[10], and loss-of-function alleles seem to be affected more by diversification than domestication[10].

Selective sweeps[71] — that is, the reductions of nucleotide variation that result from strong selective pressures acting on particular loci — have been observed in genes associated with domestication or diversification phenotypes. The best example of a domestication-related selective sweep occurs at the maize gene *tb1*, which is involved in the suppression of axillary-branch formation, where a selective sweep ~90 kb in length across the promoter and proximal intergenic region has been observed[72] (Fig. 5). Other examples include a 600-kb selective sweep[73] at the maize gene *Y1*, involved in the yellow-kernel phenotype, and a 260-kb sweep in the rice gene *waxy*, which is associated with low-amylose rice in northeast Asian cultivars[57] (Fig. 5).

The strength of selection on the loci affected by domestication and diversification can be estimated from the physical extent of a sweep[57]. Using this approach, inferred selection coefficients, s, for cases of natural selection range from 0.02 to 0.70, the latter being associated with drug resistance in the parasite *Plasmodium falciparum*[57]. For maize *tb1*, which is the only domestication locus for which the selection coefficient has been estimated, s is in the range 0.05–0.20, comparable to cases of natural selection. By contrast, the crop diversification genes *waxy* in rice and *Y1* in maize have higher selection coefficients ($s>1$). This may simply reflect differences in recombination rates or the relatively recent selection for diversification compared with domestication, but it may also suggest that stronger selection accompanies post-domestication diversification of crop phenotypes[57].

Combining phylogeographical analysis with molecular genetic analysis allows researchers to determine which geographical regions gave rise to various traits and to chronicle the spatial spread of alleles subject to Darwinian selection. The analysis at the rice *waxy* gene, for example, demonstrates that the causal glutinous rice polymorphism had a localized origin in Southeast Asia and subsequently spread to northeastern Asia, where it is culturally valued[56]. Another study reveals that the loss-of-function allele of the rice *Rc* gene, which encodes a basic helix–loop–helix protein and gives rice the white pericarp favoured by most Asian cultures, probably originated in tropical *japonica* rice in Southeast Asia but spread into the *indica* rice variety that is found primarily in southern Asia[74].

Solving an obscure problem

As Darwin noted in *On the Origin of Species*[3], adaptation to a cultivated environment or human cultural preferences — “man’s use or fancy” — is one of the hallmarks of domesticated species, an observation that served him well when he formulated his theory of natural selection. In the 150 years since, both archaeology and genetics have provided crucial insights into the nature and timing of domestication, which

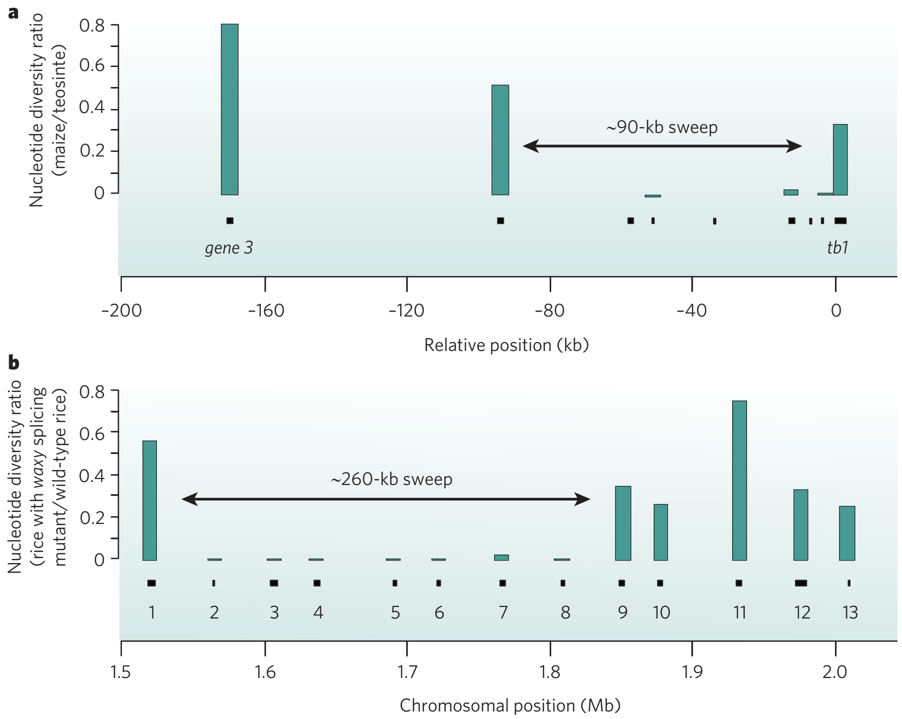

Figure 5 | Examples of selective sweeps at the maize gene *tb1* and at the rice locus *waxy*. Selection leads to a sweep region that appears as a region of reduced nucleotide diversity in the genome. Black boxes indicate the positions of sequenced regions relative to the maize gene *tb1* (**a**) and the physical positions of the sequenced regions on rice chromosome 6 (**b**). Green rectangles show the ratios of nucleotide diversity at these regions between maize and teosinte (**a**) and between rice accessions with the splicing mutant of *waxy* and wild-type rice (**b**). Sequenced regions in **b** include hypothetical genes (1, 2, 6 and 9), expressed sequence tags (4 and 10), the *waxy* locus (7), and loci that encode a receptor-like protein (3), glycosyl hydrolase (5), transketolase (8), enolase (11), a kinesin-like protein (12) and ribosome-binding factor A (13). The estimated extent of the selective sweep is indicated by the arrows.

underpinned the Neolithic revolution and gave rise to agrarian societies (which became the dominant *H. sapiens* cultures). The extent to which domestication differs from natural selection on wild species remains to be understood, as well as whether these processes are simply part of a continuum of selective regimes, differing merely in type and intensity but conceptually identical. To what extent does parallel evolution affect the same genes across multiple species during domestication and diversification? How can archaeobotanical evidence constrain molecular, evolutionary and genetic models of domestication by providing more realistic estimates of the time span for the evolution of these domestication traits, as well as the timing and strength of selection events? Can we combine archaeological data with genomic information to track the timing and geographical origins of traits? Answering these and other questions requires continued work to isolate more domestication and diversification genes, and more-systematic archaeological studies are needed to provide a comprehensive picture of the origins and dynamics of domestication.

Even now, 150 years after the publication of Darwin's most influential work, domesticated species are some of the best-studied examples of evolutionary diversification, and archaeological and genetic investigations of this unique case of plant–animal co-evolution have provided some of the most comprehensive views of species diversification. The case Darwin made in *On the Origin of Species* remains true: the study of domestication is central to understanding the nature of what Darwin referred to as "the obscure problem" of natural selection. ■

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