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Domestication as Innovation: The entanglement of techniques, technology and chance in the domestication of cereal crops

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Abstract

The origins of agriculture involved pathways of domestication in which human behaviours and plant genetic adaptations were entangled. These changes resulted in consequences that were unintended at the start of the process. This paper highlights some of the key innovations in human behaviours, such as soil preparation, harvesting and threshing, and how these were coupled with genetic 'innovations' within plant populations. We identify a number of 'traps' for early cultivators, including the needs for extra labour expenditure on crop-processing and soil fertility maintenance, but also linked gains in terms of potential crop yields. Compilations of quantitative data across a few different crops for the traits of nonshattering and seed size are discussed in terms of the apparently slow process of domestication, and parallels and differences between different regional pathways are identified. We highlight the need to bridge the gap between a Neolithic archaeobotanical focus on domestication and a focus of later periods on crop-processing activities and labour organization. In addition, archaeobotanical data provide a basis for rethinking previous assumptions about how plant genetic data should be related to the origins of agriculture and we

contrast two alternative hypotheses: gradual evolution with low selection pressure versus metastable equilibrium that prolonged the persistence of 'semi-domesticated' populations. Our revised understanding of the innovations involved in plant domestication highlight the need for new approaches to collecting, modelling and integrating genetic data and archaeobotanical evidence.

Introduction

The transition to farming is often regarded as the most significant threshold in recent human cultural evolution, allowing unprecedented population growth and providing the potential basis for surplus production that underpinned urbanism and civilization. It is also increasingly linked to a major threshold in the use of material symbols (e.g. Hodder 2004). In cultural terms, innovations can be understood as trying something new, and agriculture results from a series of human behavioural innovations. In biological evolution, innovation is often understood in terms of new genetic variants (mutants) with distinctive morphological consequences (phenotypes) which offer new adaptive opportunities to a plant or animal (Fisher 1930). Cultivation itself was a new technique, a strategic shift in human behaviour, and this had unintended consequences in terms of favouring genetic innovations in cultivated plant populations, adaptations often glossed as the domestication syndrome (Harlan et al. 1973; Hammer 1984).

The emergence of the first domestication traits would have had consequences for the productivity of early cereal exploitation practices, and required or encouraged further human behavioural innovations. These in turn will have altered the selection pressures on genetic variants within crop populations and selected for further genetic innovations. Thus, there was inevitably an entangled process of behavioural and genetic innovation, response and further response. This implies that

evidence for changes in crops, i.e. the emergence of domestication traits, are linked to changes in cultural practice, and it was sequences of these linked innovations that formed the pathways between hunting-and-gathering lifeways to fully agricultural societies and to the populations of domesticated cereals we rely on for sustenance today. These pathways may have taken several centuries to millennia, and might have involved plants that were "semi-domesticated" (an idea we return to below) and economies that were intermediate (Harris 2009) between foragers and agriculturalists. This paper will compare domestication pathways involving differing cereal crops in different world regions, especially Near Eastern wheat and barley, Chinese rice, and African pearl millet, for insights into recurrent and variable sequences of innovation at the start of agriculture and will highlight continuing archaeological questions.

The behavioural and ecological matrix of domestication

Cultivation is a human activity, while domestication consists of genetic and morphological changes within the plant that people cultivate. While this simple contrast has long been recognized in archaeobotany (e.g. Harris 1989; Hillman and Davis 1990), it hides a more complex set of interrelationships between human activities, modified habitats and genetic changes in plant populations. In addition to crops, weedy and feral forms of the same species evolved in human impacted environments. Changes in genes can be attributed to changes in habitats, which in turn are the result of innovations in human practice.

Because it is the least ambiguous, "hard" domestication traits of seed crops, are the clearest archaeological indicator of cultivation, but it must be kept in mind that these are a result, not a starting point in what was likely a long chain of innovations that constitutes a domestication pathway. The classic 'hard' domestication traits are non-shattering in cereals, visible in the rachis

or spikelet base, and the loss of germination inhibition, often visible in the seed coat in other seed crops. But the presence (i.e. predominance in cultivated populations) of these traits must be viewed as marking the end of a process of biological evolution. Before domestication traits dominate the population, we consider the plants to still be under pre-domestication cultivation.

Other traits gradually evolve under cultivation, coming to dominate whole populations, but are ambiguous characteristics of domestication on an individual plant by plant basis. One such trait is seed size increase. The very beginnings of cultivation, before there have been any appreciable morphological changes, may be inferred from weed flora, as has been argued for the Levantine Pre-Pottery Neolithic A [PPNA] (Colledge 1998; Willcox et al. 2008)— and perhaps earlier at Epipalaeolithic Abu Hureyra (Hillman et al. 2001; cf. Willcox et al. 2009). What recent evidence for these changes implies is that there were a number of different transitions that require causal explanation. The initiation of cultivation is perhaps the key behavioural change in humans, but the more difficult to detect in its incipient form. Subsequent progressive forms of pre-domestication cultivation require behavioural shifts that constitute intensification and may include innovations in soil preparation (tillage, irrigation, manuring), while shifts in harvesting and crop-processing will have been necessary responses to changes in the morphology of pre/early domesticated plants. The order of these innovations may vary, and documenting this variation and explaining it must be a focus of research in agricultural origins. In the sections that follow we will review the archaeology and genetics of some of these changes and the human behavioural innovations that are implicated in their evolution.

Non-shattering and the agricultural labour trap

Archaeobotanists and agricultural botanists have focused on the loss of natural seed dispersal for decades. Although this distinction between wild and cultivated populations had been recognized by Vavilov (1950), it was the botanical studies of Zohary (e.g. 1969), Harlan et al. (1973) and the archaeobotanical studies of Helbaek (e.g. 1969) which drew prominence to it. Often based on just a single mutation, grasses can lose the ability to form the abscission scar on which wild type seed dispersal depends (fuelled largely by gravity, wind and moisture variation: Elbaum et al. 2007). This makes them essentially dependent upon the human farmer to disperse the grain, which involves manual separation of the spikelets (threshing) and planting. From the point of view of the cultivator, gains are made in terms of higher yields, as the farmer can wait until all, or most, of the grains on a plant have matured, whereas within mixed populations of shattering and non-shattering plants the harvester would have had to balance loss of grain through shedding, as they matured, with reduced yields through grains harvested immature (i.e, before spikelets have filled entirely). This would have been a particular problem with cereals which had a long period of grain maturation across populations, such as millets or the better documented case of rice (Fuller et al. 2007). Even in modern cultivated rice under traditional cultivation there is a balance to be reached between losing grains that shatter as spikelets dry and "over-mature" versus harvesting too early before all the grains have filled (Horiuchi et al. 1971), and such potential losses would have been much more severe in undomesticated or semi-domesticated populations.

Cultivation is not only about controlling the space over which cereals are distributed but also their temporal distribution. The transition from wild to domestic cereals sees a narrowing in the period of availability (ripening), perhaps from a few months to one or a few weeks. This has a further implication, that more evenly-ripening cereals may initially present a "labour bottleneck", in the sense of requiring that the harvest is brought in over a relatively short intensive period. This would have clearly been the case where even-ripening developed as a result of cultivation. Sedentism and

the protection of crops would have reduced grazing, and might have favoured taller cereals. In an experimental study of wild emmer wheat it was found that clipping (which simulates grazing) favoured lower growing, less straight plants with more tillers and staggered ripening (Noy-Meir and Briske 2002). The reduction in grazing pressure in itself should result in taller plants and in a more even seeding time and germination pattern.

It may be in this context that experimentation with harvesting methods, and perhaps new technologies like the sickle, should be seen. Ethnographic reports suggest that hunter-gatherers are likely to have gathered wild cereals, at least those with panicles (like rice or millets) by beating or basket swinging (Harris 1984; Harlan 1989), or cutting and pulling while still green and allowing plants to dry in heaps which allows wild type abscission to occur gradually, as practiced by some Australian Aborigines with wild *Panicum* (Allen 1974). Experimentally, cutting (while green but near-mature) was a more effective strategy for wild, eared cereals, like wheat and barley (Willcox 2007). While most grasses and wild cereals would require labourious dehusking (and subsequent winnowing), such collection methods and wild-type abscission would not require a threshing to separate spikelets from the ear/panicle and straw. This implies that at some point during pre-domestication cultivation, as non-shattering types increased in proportion to wild types, people fell into a "trap" of new work: threshing and winnowing (Figure 1). Domesticated cereals, once dried, do not shatter but must be physically separated, and thus require 'early' crop-processing stages (threshing and winnowing, sometimes with the use of sieving). Crop-processing has long been a research interest of archaeobotanists (e.g. Hillman 1981; Jones 1987; Harvey and Fuller 2005), but few have tackled the dynamics of how threshing and winnowing (early processing stages) emerged as the result of new morphogenetic adaptations of domesticated cereals and a new labour cost of cultivation. If the evolution of domestication traits was the unintended consequence of how humans cultivated and harvested early crops, then a knock-on effect, presumably also unintended, was the

addition of these early stages of crop-processing. Dehusking was likely more arduous than threshing, but the extent to which additional scheduling demands for this early stage added to scheduling constraints deserves consideration. The experimental data of Willcox (2007) suggests that this may have required minimal additional effort in the case of early wheat and barley. By contrast with cereals like rice and millet this might have been a more significant shift. Nevertheless, as shown for later agricultural societies, such as Iron Age Britain or the Bronze Age Indus (Stevens 2003; Fuller and Stevens 2009), communities can be divided on the basis of whether threshing was normally organized before storage or was carried out piecemeal across the year, suggesting that the labour of threshing was still significant in the context of other seasonal demands. For example, the period of early rice harvests in China would have overlapped with the peak season for the collection of acorns and other wild nuts (cf. Fuller and Qin 2009), whereas early wheat and barley harvests and processing might have to be balanced against the peak hunting season of gazelle and onager (Moore et al. 2000).

A methodological issue still to be tackled is how to recognize the emergence of threshing and winnowing from earlier wild-type harvesting and processing sequences. A first step is to document the emergence of the non-shattering adaptation, to provide the necessary time scale against which chaff and weed assemblages can be studied. Then one can consider how and when crops were stored and processes, e.g. were non-shattering ears stored as such or were they threshed at harvest? Indeed, the tracing of such patterns is likely to play an important role in understanding how non-shattering as opposed to shattering grains or spikelets eventually came to be those that were sown to produce the following seasons harvest.

In the past few years quantitative archaeobotanical evidence has begun to allow us to track the evolution of non-shattering cereals through the study of preserved chaff remains (Tanno and

Willcox 2006; Fuller 2007; Fuller et al 2009). The indication of these data is that our prior assumption that non-shattering, domesticated mutants will rapidly become fixed in cultivated populations (Hillman and Davis 1990), is incorrect. Rather we need to think in terms of domestication as protracted pathways and discard the notion of "domestication events". Interestingly, the available data, from wheat, barley and rice, suggests very similar rates of change even though starting dates were different (Figure 2). The total time length of pre-domestication cultivation remains unclear. Inferences for the start of pre-domestication cultivation, for example from weed flora (in the Near East) or landscape management (in the Lower Yangtze) suggest that there was an extended period of perhaps two (or more) millennia of cultivation prior to the start of recognizable selection for non-shattering. This raises the question as to what factor led to the key change through which non-shattering began to evolve. While archaeologists tend to attribute this to a change in harvesting practice, other constraints should be considered. For example, chance constraints on population genetics may be significant when early crops were relatively small subpopulations within a larger landscape of wild progenitors (Jones and Brown 2007). Early cultivars should perhaps be thought of as invading populations, in which it is expected that introgression will result mainly in geneflow from the local population (wild progenitors) into the smaller invading populations (crops) (cf. Currat et al. 2008).

Further we might ask how labour organization may have impacted harvesting and processing practices. For example, could a choice not to invest efforts in time-consuming threshing and winnowing have encouraged early cultivators to return to gathering wild cereals to bolster their grain stores? This in turn depends on the availability and distance to wild stands. At present, there is a tendency to focus on crop domestication as a biological process, whereas the archaeobotany of post-domestication periods asks more questions about labour organization and crop-processing (e.g.Van der Veen 2007; Fuller and Stevens 2009). What we need, is to bring these two aspects of

archaeobotanical research together, since the human practices of cultivation, harvest and processing are entangled with the domestication process.

Harvesting and the soil nutrient trap: implications of apical dominance

Another less often discussed change is the development of a more erect growth habit. This has attracted particular attention in rice genetics recently, since a gene known as PROG1 has been identified. It appears to have a large effect on plant morphology (Tan et al. 2008; Jin et al. 2008), changing the low and outwards-growing rosette of the wild plant into the taller, straighter form typical of the crop (contrasted schematically in Figure 1). As explored in broader comparative terms by Doust (2007), domesticated cereals in general have shifts from their wild progenitors, sometimes involving suppression of tillers (basal secondary stalks) or axillary branches higher up, but also often selecting for even maturation across different branches. For example, in maize, sorghum or millets (e.g. *Setaria italica*, *Pennisetum glaucum*), the domesticated form tends to have suppression of any lateral branches or tillers, whereas in wheat, barley and rice lateral branching is reduced but tillers have been selected which mature more evenly.

Branching, however, is not determined entirely by genes but also responds to the environment. Most grass culm nodes have the potential to grow into branches but the branches are suppressed by hormones which are responsive to environmental factors like shading (light resources) or density of plants (affecting water and mineral resources). Experiments with foxtail millet and its wild progenitor (*Setaria viridis*) found that the number of spikelets and of primary branches both increased under low density planting (Doust et al. 2005). While the crop and its wild progenitor differed substantially from each other, indicating genetically controlled differences, both responded to environmental conditions similarly. Similar responses are reported for maize (Moulia et al. 1999).

For the early cultivator/farmer the significance of this is that less crowded plants, with better access to soil space (water and nutrients) and light, tend to grow into more productive crops. This implies that a likely constraint, and thus a pre-requisite, on the evolution of erect and productive forms may be that early farmers are finding or maintaining improved soils. Thus rather than being an immediate adaptation of incipient cultivation, more erect crops came after farmers had begun to fertilize and manage soils, which would have resulted in increased bushiness. In this context mutations (like *PROG1* in rice) would have created tall, productive, less bushy plants that could be selected easily through harvesting methods (like panicle cutting), or conscious selection. In the case of rice, this is likely to be linked to the emergence of practices of making and maintaining labour-demanding paddy field systems, an innovation which can be placed, on current evidence, near the end of the domestication process and not before 4500-4000 BC (Fuller and Qin 2009). Similarly, in the Near Eastern and European Neolithic there is mounting evidence that early plots were intensively managed and probably manured (Bogaard 2005).

Early Agricultural Gains: grain size, number and germination

Another aspect of morphological change with domestication, and perhaps the most widely studied, is increased seed size. There is a growing database for wheat and barley from the Near East suggesting that increased grain size began in PPNA and continued through to the end of the Late PPNB (Figure 3, top). Comparable data is available for several crops in other regions, including rice and West African pearl millet (*Pennisetum glaucum*) (Figure 3). There is general similarity in the gradual rate of change, from which we conclude that there was a parallel selection for larger grains. Minor discrepancies, such as a delay in grain size increase until after non-shattering in pearl millet, suggest that differing pathways of human innovations may have occurred with different crops.

There are three competing hypotheses for changes in grain size. Size may have been a plastic response to the improved soil conditions of cultivation, which lead to better grain maturation (Willcox et al. 2008: 322). It is also possible that larger-grained varieties were introduced from elsewhere (ibid.), presumably with larger grained ancestors. The latter line of reasoning, that different grain sizes represent different varieties moved mainly by the vagaries of human migration, seems preferred by Liu et al. (2007: 1066) in their consideration of Chinese rice (to explain size increase at Longqiuzhuang). Alternatively, as was hypothesized by Harlan et al. (1973), grain size should increase as a product of genetic adaptation to soil disturbance and deeper burial with cultivation (Smith 2006; Fuller 2007). Larger seed size may be adaptive in several ways, improving competition in early growth patches and survival of the seedlings despite stresses such as herbivory or deeper burial (Maranon and Grubb 1993; Moles and Westoby 2004). That increase in seed size does not require that plants are non-shattering is indicated by the existence of weedy/commensal varieties that are large-grained like the crop but prone to shattering like true wild progenitors: such weeds are reported for several Indian millets (*Paspalum scrobiculatum, Echinochloa colonum, Setaria pumila, Brachiaria ramosa*) (Kobayashi 1987; 1989). Recent genetic work on rice has identified a recessive mutations that seems to affect grain width by affecting the size and row of husk cells (Shomura et al. 2008), and another that causes longer grains and higher grain weight (Fan et al. 2006). Similar mechanisms are likely in other seed crops. While both size and number of seeds will doubtless show plasticity, as is true of branching, the trait of seed size seems likely to have shown the directional change under selection by early cultivation.

Whatever the case may be, the increase in grain size represents an increase in yield, a gain from the point of view of the incipient farmer. Unlike the evolution of non-shattering or erect plants, this is one trait that may provide inherent returns without requiring more labour commitment, and for this

reason it need not be surprising that it may be grain size increase that evolved first in some cases. In other cases, for species such as pearl millet (Fuller 2007: 920), or tef (D'Andrea 2008) early gains in yield may have had more to do with the increase in seed number in individual spikes, which might have delayed the impact of selection of grain size.

Semi-Domestication: A meta-stable equilibrium?

Our standard model has been that there was directional selection for domestication trait(s), with increasing frequency of domestic-type alleles (genes for non-shattering) within the population, moving continually towards fixation. In which case, the result is an S-shaped curve (Fig. 4), with a rapid transition equating to a short timescale (e.g. 20-200 years). Weaker selection, which fits current archaeobotany better, equates to a longer timescale (1000 years or more). As suggested by Willcox et al. (2008) this could also result from recurrent bolstering of stored harvests with wild collected grains, which amounts to reducing the overall strength of selection. However, the sum total of archaeobotanical data points (quantified assemblages) is still rather small, and this limited empirical dataset could fit to several potential models.

This raises the question of whether we might consider that semi-domesticated populations were maintained in a metastable equilibrium (Fig. 4). In this model, the initiation of cultivation and/or new harvesting methods should allow adaptations to emerge in the crop population and perhaps rapidly increase, but to a fairly stable minority balanced against persistence of wild adaptations. If cultivation plots are shifting, or left fallow, then there is a continued advantage for plant populations to maintain wild type dispersal, i.e. for weedy/feral adaptations. When one plot is abandoned, shattering types will grow up ('volunteers'), but non-shattering types may have an advantage in the harvested seed corn population that people plant. Both types will have selection for human-impacted traits, such as germination characters (increasing grain size and loss of

dormancy), and thus we would expect strong directional selection in these traits. A few crops (e.g. *Brachiaria ramosa*, *Setaria pumila*, *Panicum sumatrense*) are reported to have limited degrees of non-shattering amongst cultivars and frequent shattering amongst weedy/commensal types (Kobayashi 1987; 1989). Such crops may provide a model for 'intermediate' early cultivars that are likely top have existed for some period in the history of every cereal species. This raises the question whether there are parameters, in terms of seeded field size, yield, harvesting efficiency, and field rotation frequency that would maintain selection for a meta-stable equilibrium of part-domesticated populations? This question calls for careful modelling, which should be possible through computer simulations (e.g. Allaby et al, 2008; Currat et al. 2008), but more complex than those which have been hitherto used. A further question concerns the tipping point: what pushed an 'intermediate' equilibrium towards full domestication? Was it changes in cultivation/ processing practice? Another possibility in light of a protracted transition is that mutations that had already evolved in another region were transferred through grain exchanges, representing a merging of domestication pathways that began separately.

Tipping the balance: chance and intention in innovation

As we have explored, the crop domestication process includes several distinct but entangled processes, some of which have an inevitability about them: unintended consequences of interactions between humans and proto-cultigens. We have referred to some of these consequences as "traps," as they result in human farmers having to expend extra effort, e.g. on crop-processing or maintenance of soil fertility. This probably implies that compared to their ancestors who made the very first steps in cultivation or who were hunter-gatherers, farmers became increasingly entangled into more labour-demanding food production regimes. The domestication pathway involved several 'tipping points' of intensification. This is so because morphologically domesticated cereals require more labour, both in terms of investments in cultivation (the soil nutrient trap) and in post-harvest

labour (the crop-processing trap). The payback for this, however, is increased reliability in harvest and increased yield, and more controllable (owned) resources.

This may have implications for the paradigm within which researchers have been thinking about agricultural origins for the past few decades. In the 1960s, a major paradigm shift occurred as ethnographic foragers were seen to expend little labour in their subsistence by comparison to farmers (e.g. Lee 1968), which lead to what Sahlins (1968) dubbed "the original affluent society". This has led to a paradigm in which the origins of agriculture had to be explained mainly as driven by a push, due to environment and demography, that forced people to work harder to feed themselves. But might it be the case, as the protracted transition to agriculture becomes somewhat clearer, that the very first steps may have been of time efficiency, as implicated by some "diet breadth models" (e.g. Winterhalder and Goland 1993; Piperno 2006), or the result of social choice, e.g. along the lines of the "scheduled availability model" of Marshall and Hildebrandt (2002). It was only later, as the unintended entanglements set in that early cultivators slipped into the traps of greater labour costs and greater, largely irreversible, reliance of food production? The 'non-affluence' of small-scale farmers was as much an unintended consequence of the entangled domestication pathway as was the non-shattering ear.

Acknowledgements

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Figure captions

Figure 1. A schematic diagram comparing the crop-processing stages of domesticated crops and wild harvested crops, in this case rice. A key development with domestication is the need for early processing stages (threshing and winnowing) with implications for the formation of weed assemblages and the presence of immature grains and immature spikelet bases.

Figure 2. Archaeobotanical rachis/ spikelet base data indicating the slow fixation of domesticated (nonshattering) cereals, aligning data from Near Eastern wheat and barley with Lower Yangtze rice in terms of the domestication trajectory modelled as a straight line trajectory (after Purugganan and Fuller 2009). Arrows indicate other lines of evidence for inferring presence of cultivation, during the PPNA (e.g. Colledge 2001; Willcox et al 2008), Late Epipalaeolithic Mureybit (Mur), for which weed flora suggests cultivation (Colledge 1998), and more questionably Abu Hureyra 1 (AH) (see Hillman et al 2001; cf. Willcox et al 2009). For the Lower Yangtze these include the evidence for land management and some domesticated spikelet bases from Kuahuqiao (KHQ) (Zheng et al 2007; Zong et al 2007), and more questionably the microcharcoal record at Loujiang (LJ) (Atahan et al 2008)..

Figure 3. A comparison of trajectories of grain size increase in barley, wheat, rice and pearl millet. Shown are the mean and standard deviation of grain breadth for measured assemblages plotted against a median estimate of age. Replotted based on data in Fuller (2007) and Fuller and Allaby (2009).

Figure 4. At left the standard sigmoidal curve for the domestication process, in which the trajectory approach a linear regression of proportion domesticated against time. The rapid domestication model that was is indicated by the upper timescale, and a protracted transition model indicated by the lower timescale. At right, an alternative "meta-stable semi-domestication " model, in which protracted, but dynamic,

transition is envisioned: an intermission of meta-stable equilibrium is reached, caused by a balance of differing selection pressures in cultivated and wild populations with gene-flow. Human practices of harvesting and processing may be crucial to either maintaining this equilibrium or pushing it past the tipping point of domestication.

Illustrations for manuscript of Fuller & Allaby [include Chris?]

Domestication as Innovation: The entanglement of techniques, technology and chance in the evolution of the domestication syndrome in early seed crops.
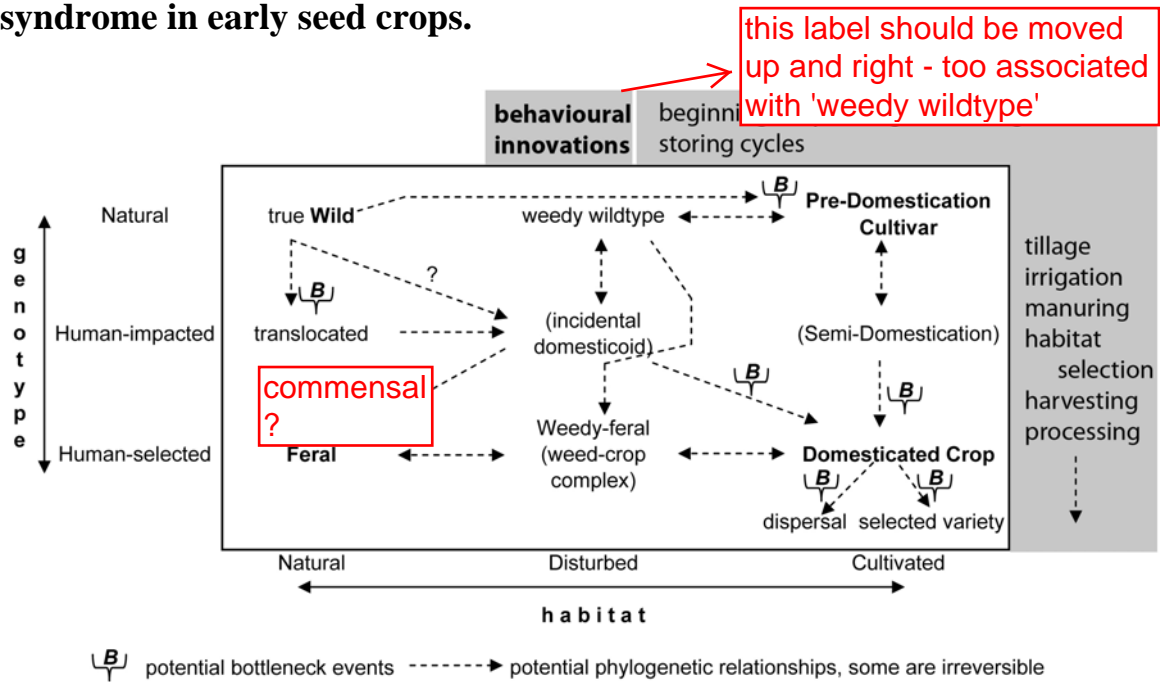
Figure 1. Evolutionary trajectories between wild and domesticated, and intermediate, plant types, defined against a matrix of habitat (more or less human-impacted) and plant genetic changes (more or less human-impacted). Indicated are all of this transitions that theoretically may produce genetic bottlenecks, and thus contribute to patterning in genetic diversity. Some transitions are theoretically reversible or irreversible. Any of these transitions may be considered to involve genetic "innovation". Indicated around the outside of the matrix in grey are human behaviorual innovations, which determine the position of a plant population on the axis of genotype and habitat type.
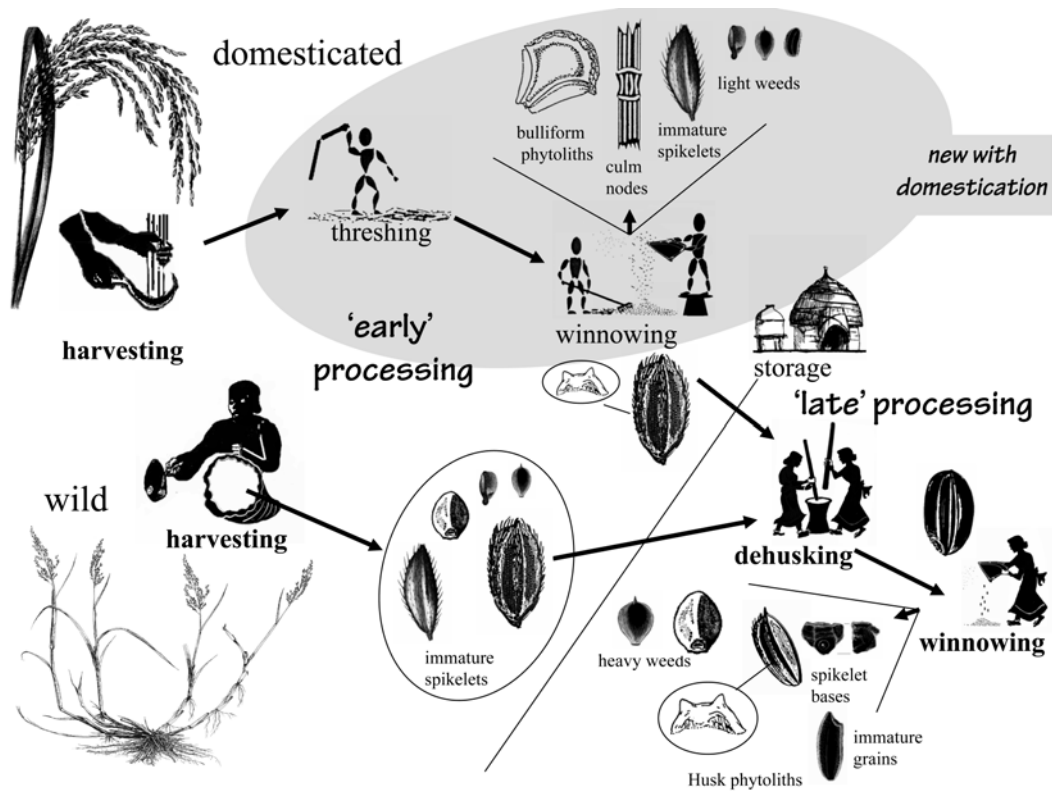
Figure 2. A schematic diagram comparing the crop-processing stages of domesticated crops and wild harvested crops, in this case rice (developed from originals in Stevens 2003; Harvey and Fuller 2005). A key development with domestication is the need for early processing stages (threshing and winnowing) with implications for the formation of weed assemblages and the present of immature grains and immature spikelet bases.
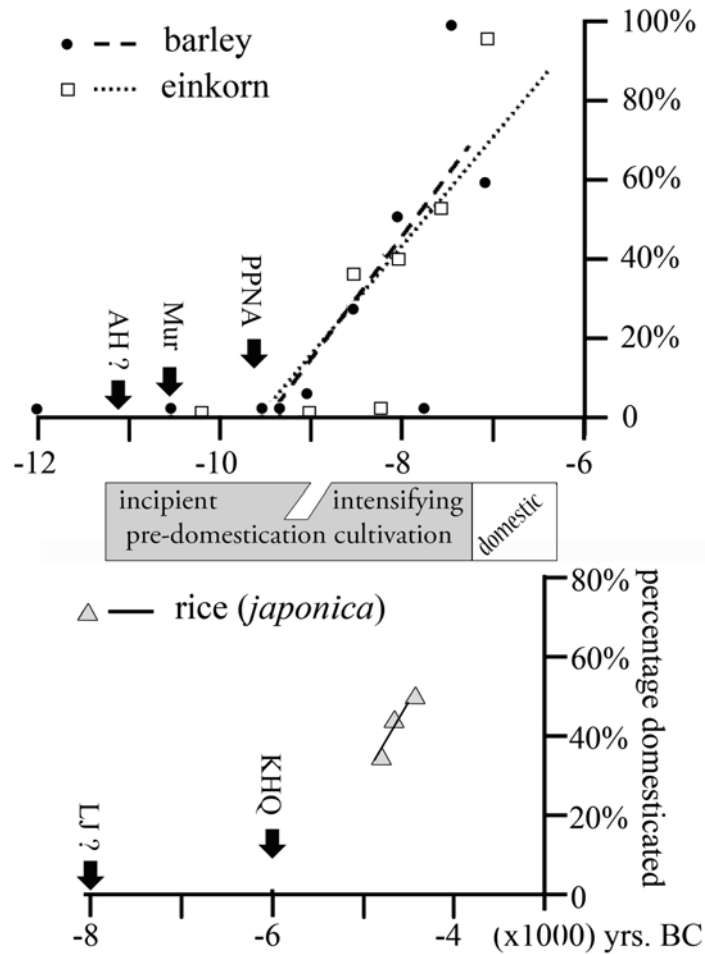
Figure 3. Archaeobotanical rachis/ spikelet base data indicating the slow fixation of domesticated (non-shattering cereals), aligning data from Near Eastern wheat and barley with Lower Yangtze rice in terms of the domestication trajectory modelled as a straight line trajectory (after Purugganan and Fuller 2009). Arrows indicate other lines of evidence for inferring presence of cultivation. In the Near East these include the start of the PPNA, when cultivation is widely inferred (e.g. Colledge 2001; Weiss et al 2006; Willcox et al 2008), Late Epipalaeolithic Mureybit (Mur), for which weed flora suggests cultivation (Colledge 1998), and more questionably Abu Hureyra 1 (AH) (see Hillman et al 2001; cf. Willcox et al 2009). For the Lower Yangtze these include the evidence for land management and some domesticated spikelet bases from Kuahuqiao (Zheng et al 2007; Zong et al 2007), and more questionably the microcharcoal record at Loujiang (LJ) (Atahan et al 2008), and the archaeobotanically poor Shangshan (Liu et al. 2007); for discussion see Fuller and Qin (2009). The approximate durations of incipient and intensifying pre-domestication, referred to in the text, are indicated. Primary data for einkorn and barley data-points is compiled in Fuller (2007, Fig. 5). Primary data for rice represents the estimated "domesticated upper limit" (from Fuller et al 2009, supplementary on-line material).

[to add]…
Figure 4. A comparison of trajectories of grain size increase in barley, rice and pearl millet.
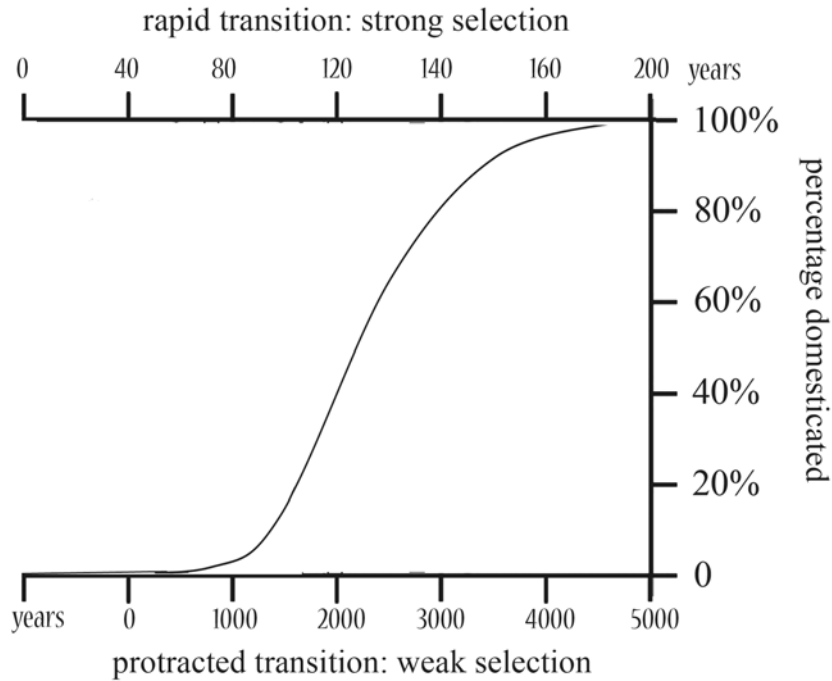
Figure 5. Our standard sigmoidal curve for the domestication process, in which the trajectory approach a linear regression of proportion domesticated against time. The rapid domestication model that was suggested by Hillman and Davis (1990) is indicated by the upper timescale, but this is now giving way to a protracted transition model indicated by the lower timescale. The latter assumes a straight forward gradual domestication process but with weaker selection pressure (e.g. Fuller 2007).
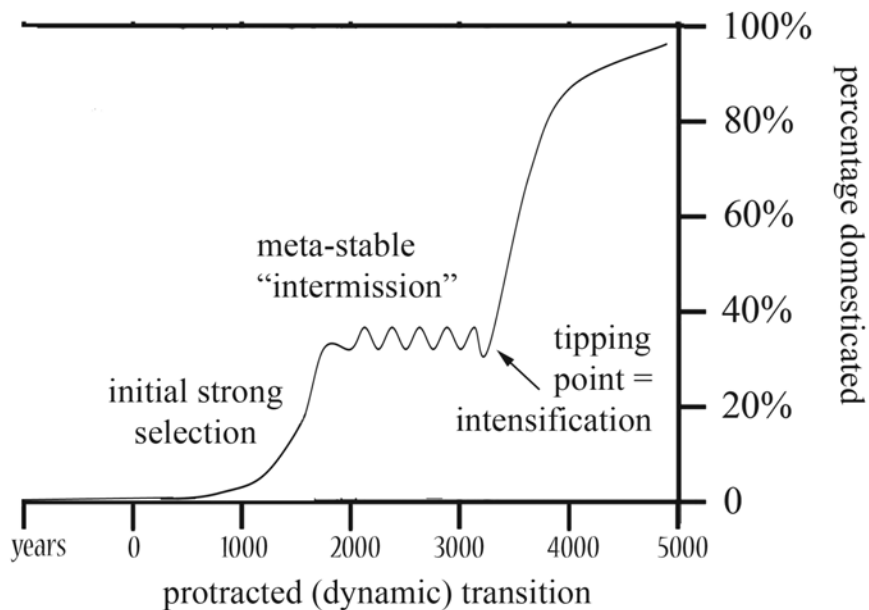

Figure 6. An alternative "meta-stable semi-domestication" model, in which protracted, but dynamic, transition is envisioned. A period of meta-stable equilibrium, or "intermission," is reached at a moderate level of domesticated genotypes (a minority ?). This may be caused by a balance of differing selection pressures in cultivated and wild populations with geneflow. Human practices of harvesting and labour expended on processing may be crucial to either maintaining this equilibrium or pushing it past the tipping point of domestication. In this case the initial start towards the meta-stable equilibrium and the final push to full domestication may both have occurred under strong selection and rapid processes closer to that modelled by Hillman and Davis (1990) than the long, slow weak selection inferred by Fuller (2007).