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Archaeogenomic insights into the adaptation of plants to the human environment: pushing plant–hominin co-evolution back to the Pliocene

Robin G. Allaby [a,*], Logan Kistler [b], Rafal M. Gutaker [a], Roselyn Ware [a], James L. Kitchen [c], Oliver Smith [a], Andrew C. Clarke [a,d]

[a] *School of Life Sciences, Gibbet Hill Campus, University of Warwick, CV4 7AL, United Kingdom*
[b] *Departments of Anthropology and Biology, The Pennsylvania State University, University Park, PA 16802, USA*
[c] *Rothamsted Research Station, Harpenden, Hertfordshire AL5 2JQ, United Kingdom*
[d] *McDonald Institute for Archaeological Research, University of Cambridge, Downing Street, Cambridge CB2 3ER, United Kingdom*

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ABSTRACT

The colonization of the human environment by plants, and the consequent evolution of domesticated forms is increasingly being viewed as a co-evolutionary plant–human process that occurred over a long time period, with evidence for the co-evolutionary relationship between plants and humans reaching ever deeper into the hominin past. This developing view is characterized by a change in emphasis on the drivers of evolution in the case of plants. Rather than individual species being passive recipients of artificial selection pressures and ultimately becoming domesticates, entire plant communities adapted to the human environment. This evolutionary scenario leads to systems level genetic expectations from models that can be explored through ancient DNA and Next Generation Sequencing approaches. Emerging evidence suggests that domesticated genomes fit well with these expectations, with periods of stable complex evolution characterized by large amounts of change associated with relatively small selective value, punctuated by periods in which changes in one-half of the plant–hominin relationship cause rapid, low-complexity adaptation in the other. A corollary of a single plant–hominin co-evolutionary process is that clues about the initiation of the domestication process may well lie deep within the hominin lineage.

Introduction

The exploitation of plants by humans is often viewed as a process of human dominance over plants that resulted in the domestication of many species. Such a perspective invokes a notion of passivity on the part of the plants, which may be considered to some extent 'victims' of the domestication process. Theorists have long considered the evolution of plant domestication to be a co-evolutionary process between plants and humans, in which both partners have become modified (Rindos, 1984; Harris and Hillman, 1989). Recently, evidence has accrued that this co-evolutionary process is one that stretches far further back in time than the profusion of domestications that litter the late Pleistocene and early Holocene epochs.

The plant–hominin co-evolutionary continuum

The profound influence between plants and humans is apparent deep into the palaeoanthropological record. Plants adapted to the gradual cooling environment of the Neogene with the rise of many C4 lineages in parallel (Christin et al., 2011; Sage et al., 2011), with the grasses in particular predisposed to C4 evolution (Christin et al., 2013). The expansion of C4-dominated savannahs during the cooling latter stages of the Pliocene 2.8–2.4 mya (millions of years ago) is associated with an increase in the consumption of C4 foods in the diet of hominins such as *Australopithecus afarensis*, reflecting a greater dependence on warm season grasses and sedges as well as C4-grazing animals (Sponheimer and Lee-Thorp, 1999; Sponheimer

et al., 2005, 2013; Lee-Thorp et al., 2010; Wynn et al., 2013; Cerling et al., 2013a, b). Whether this shift involved an increase in the direct exploitation of plants is still unknown, but the dietary shift of the time has been associated with major episodes in brain and digestive evolution in the genus *Homo* (Aiello and Wheeler, 1995). The hominin lineage departs from the rest of the hominids in part with a change in the interaction with plants. The increased use of stone tools enabled access to richer carbohydrate sources through both retrieval and processing, for instance through digging up roots, which led to a wider spectrum of plant species utilized (Hillman and Wollstonecroft, 2014).

A quickening of the direct interaction between hominins and plants is apparent at 100 kya (thousands of years ago), with grass seed consumption by early *Homo sapiens* in Mozambique (Mercader, 2009). Later evidence comes from Neanderthals up to 50 kya where plant material enshrined in the calculus matrix of teeth shows the consumption of plants later associated with domestication, such as *Hordeum*, *Phoenix*, and members of the Faboideae (Henry et al., 2011, 2014). Furthermore, an insight into the sophistication of this plant use is evident from the occurrence of starch granules showing damage that may be consistent with cooking. This 'early' starch economy is also apparent from the late Pleistocene (13.7–15.0 kya) of modern humans from dental caries and a broad range of plant materials from the same context, including grasses, oak, legumes, pines, and pistachio (Humphrey et al., 2014).

Around 10 kya, a large number of domesticated plants emerged, characterized by a common group of traits collectively termed the domestication syndrome (Harlan et al., 1973; Hammer, 1984). The basis of this emergence has been the subject of extensive debate (Brown et al., 2009; Larson et al., 2014). Originally described as a 'revolution' (Childe, 1928), it has become apparent that these domesticated forms of plants appeared at different times in different places (Fuller et al., 2011) and became modified with domestication syndrome traits at a pace that is more consistent with natural selection than strong artificial selection (Purugganan and Fuller, 2011).

The deep history of plant–hominin interaction and the parallel and relatively gradual appearance of domesticated forms suggest that the transition of plants to domesticated forms was part of the continuum. The amelioration of climate in the late Pleistocene saw the stabilization of human niche constructs (Smith, 2007; Laland et al., 2010) facilitated by (and facilitating) activities such as cultivation of wild plant communities. Evidence is now accruing that rather than a narrowly directed artificial selection of specifically targeted species, the evolutionary trajectory of domestication is better described as an outcome of plant communities actively adapting to a human niche construct.

The adaptation of plant communities to the human environment

The emergent human environment at the end of the last glaciation led to the evolution of both domesticated and commensal species. The domestication syndrome of traits that proved to be of adaptive value to plants included the loss of natural seed and fruit dispersal, changes in seed size, increased physical and chemical palatability, loss of sensitivity to environmental cues such as photoperiod, and changes in plant architecture (Fuller, 2007). The view from the archaeological record has developed in recent years from an apparently rapid appearance of domesticated forms of crops to a hitherto unappreciated long period of pre-domestication cultivation that stretched thousands of years back into the Pleistocene (Weiss et al., 2006; Willcox and Stordeur, 2012), and a slow subsequent fixation of traits over a period of thousands of years (Tanno and Willcox, 2006).

However, it was not only plants that were exploited for food that were involved in this adaptation to live within the human environment. Other small-seeded grasses and legumes also adapted and developed domestication syndrome traits such as non-shattering and an annual habit (Spahillari et al., 1999; Senda et al., 2006; Howard et al., 2011). Therefore, a community of plants that encompassed a range beyond that which could credibly be attributed to human choice thrived in the human environment.

The human environment to which the plant communities adapted was dynamic, presenting plants with new challenges leading to new adaptations, such as with the evolution of changing agrarian practices (Fuller et al., 2010). Consequently, the syndrome adaptations of the members of this community emerged in a staggered fashion in response to different selection pressures that appeared dynamically as the human environment developed (Fuller, 2007). The changing nature of the human environment resulted in a turnover of winners and losers among domesticated species (Conolly et al., 2008). The expansion of the human environment out of centers of domestication into new latitudes then presented plant communities with acute adaptive challenges. For plants, the environment changed in terms of temperature, rainfall, and day length, particularly in Europe and Asia as crops were dispersed northwards, and also in the Americas as Neotropical crops such as maize colonized temperate zones. The dynamic nature of this co-evolutionary relationship is evident from the later crossover of some commensals to domesticate forms, such as rye that was well-adapted to northern climes (Küster, 2000).

An important emergent aspect is that domesticated plant species appear to have adapted to their community composition rather than individually as separate domesticates that could function in isolation. It is possible that some features of the domestication syndrome itself could represent the consequences of internal competition between the community species. Consequently, cultural complexes as a whole appear to have been adapted to specific ecological niches (Banks et al., 2013). Hiatuses in the spread of the human environment to new latitudes are associated not only with the time required for the adaptation of crops to new physical environments, but crucially also for the adaptation to the changing composition of the agrarian package itself (Colledge et al., 2005; Coward et al., 2008).

The challenge of understanding how plant community systems became adapted to the human environment

A new framework to understand the evolution of domestication is emerging, one in which plants adapted as a community to the human environment rather than being the passive recipients of precision targeting of individual species by humans. The latter could be considered as isolated cases. Understanding how this adaption occurred presents a major challenge, requiring approaches that consider systems level analyses, both at the community and genetic levels (Allaby, 2010; Kitchen and Allaby, 2013).

Adaptation through natural selection rarely involves a single gene. While some traits may be monogenic, such as loss of seed shattering in many cases, at any given time multiple traits are likely to be under selection. It may be tempting to regard these as independent processes, especially if the traits under consideration do not appear to be directly related. For instance, there is no expectation that seed shattering and seed size should be either controlled by overlapping genetic loci, or be traits that respond to the same environmental pressures. Although each locus under selection across a genome can be considered to involve a separate process, in reality there is a constraint on the limits of selection that can be endured. First identified and described by Haldane (1957), the cost of selection principle bridges the latter stages of the Modern

Synthesis to the Neutral Theory of Evolution (Kimura, 1968). Selection requires the differential survival of individuals. Assuming the Darwinian observation that ever-expanding populations are not sustainable, the existence of a stable carrying capacity of an environment requires that differential survival must lead to a decrease in population size (Allaby et al., 2014). Haldane calculated a consequent rate at which adaptive evolution could proceed without destroying a population or species. Haldane's principle considered a single gene model, which still stands for genes under selection. The cost argument can be extended through simulation to establish how much selection in terms of strength and number of loci that could have been endured by plants under the evolution of domestication (Fig. 1). These simulations demonstrate that only 50–100 loci across a genome could be simultaneously under selection (Allaby et al., 2014), and that selection would have to be of the order of magnitude observed under natural selection rather than the high values of artificial selection that have been suggested (Hillman and Davies, 1990). The simulations also show that the cumulative value of selection coefficients associated with separate loci, the selection load, increases with an increase in the number of loci under selection at lower selection strengths.

The models suggest a trend towards complex adaptation involving many loci, each under relatively weak selection. The more conventional view of selection, particularly of domestication syndrome traits, of a single mutant subject to a selective sweep would on the other hand achieve less selection overall, be of low dimensionality, and have the consequence of leaving the population or species vulnerable because of an inability to cope with further adaptive challenges. We would therefore expect such adaptive sweeps to occur in low complexity and essentially stable environments. A potential juxtaposition that could occur is a rapid sweeping adaptation to one or two challenges in a complex environment. In this case we would expect to have a high likelihood of population collapse as new challenges developed in the complex environment. Interestingly, patterns that fit such a juxtaposition have become evident from the archaeological record. There is a
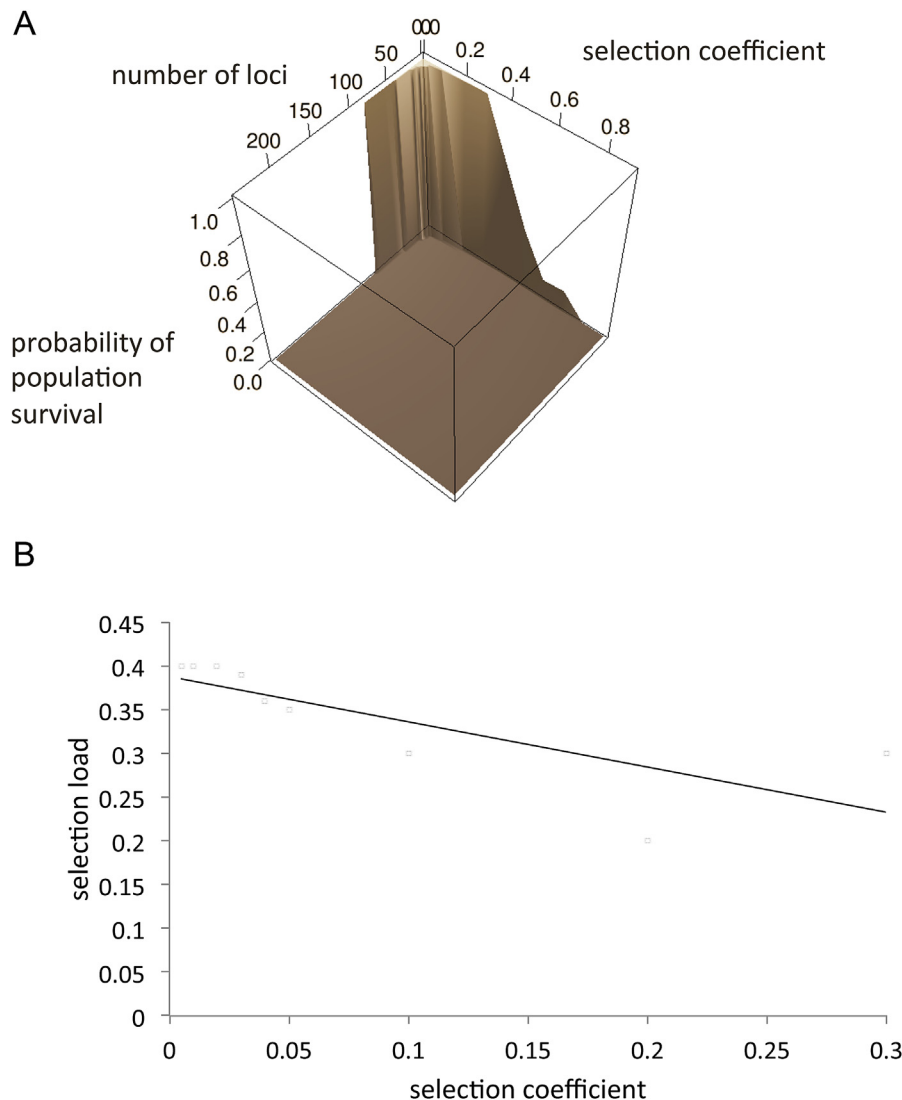
Figure 1. A. Probability landscape of population survival (p) for a given number of loci (g) under selection coefficient (s) for plant under domestication. The landscape shown is for an inbreeding population with a maximum fecundity parameter (mf) of 1.5. It is notable that the switch from survival to extinction with increasing loci number under selection is precipitous, with populations going from an estimated probability of survival of one to zero with the addition of just a few loci. In this case, a maximum of ~80 loci can be under selection before extinction occurs under the lowest value of s explored (0.005). This value is close to typical values under natural selection and to that calculated from cereals in the archaeological record (Purugganan and Fuller, 2011; Fuller et al., 2014). B. Linear regression of the maximum selection load (total amount of selection) carried across loci for different selection coefficients without any population extinction in simulations (from Allaby et al., 2014).

repeated pattern in the spread of agriculture to new environments followed by collapse shortly after (Stephens and Fuller, 2012; Shennan et al., 2013). One interpretation of this pattern is that the rapid pace of movement of agriculture into northern latitudes demanded rapid adaptation (and therefore strong selection) from the agrarian plant community. The resulting populations would have been adapting but vulnerable to further challenges, and the frequent agrarian collapse may have been precipitated by factors such as challenging seasons.

Ancient DNA as a means to understand plant adaptation to the human environment

Evidence for complex and protracted origins of many crops, particularly the cereals, is emergent from the archaeological record (Allaby et al., 2008; Fuller et al., 2014), which may echo long-term processes in the hominin lineage associated with plant processing and a consequent long-term hominin–plant coevolution. Evolutionary genetics models such as those discussed here have been applied to provide a theoretical framework for explaining how this evolutionary process could have occurred (Allaby et al., 2008, 2014). Assessment of those models requires evaluation of genomic diversity of crop plants. Extant genomes represent a palimpsest of events, including hitherto unappreciated long periods of gene flow between populations in human and non-human environments (Weiss et al., 2006; Willcox and Stordeur, 2012). Furthermore, the detection of evidence of selection from modern genomes is fraught with problems in sensitivity (Innan and Kim, 2004; Teshima et al., 2007; Yi et al., 2010). Ancient DNA provides a means of directly accessing the evolutionary process with the potential to ameliorate some of these issues.

Most of the evolution of domestication of plants occurred at relatively low latitudes, which places a constraint on the age of archaeological samples from which ancient DNA can be retrieved. Ancient DNA can currently be retrieved in useful quantities from archaeological materials up to around 4,000 years of age in North African contexts (Palmer et al., 2009), and up to ~10,000 years before the present in the subtropical Americas (Kistler et al., 2014). The advent of Next Generation Sequencing (NGS) has opened up the real possibility of utilizing ancient DNA to track genomic evolution directly and test the expectations of genetic diversity generated through models and the archaeological record. We predict from our models that there should be large amounts of change of relatively small selective value across plant genomes.

Transposable elements (TE) are DNA sequences composed of a few genes that enable a capability of self-replication and reinsertion (transposition) within the genome. Although TEs are often referred to as 'junk DNA,' in reality, transposition events have an effect on genome function by causing the genes adjacent to TE insertion points to become 'switched off' through a process of DNA methylation. One approach to test the hypothesis of large amounts of small selective value change is to monitor transposable element composition of genomes over time, assuming that the majority of transposition events are of minor selective consequence. Cotton is an example of a crop in which the evolution of genome architecture can be studied in this way, because evidence from interspecific comparisons suggests that there have been recent significant expansions and contractions of TEs (Hawkins et al., 2006, 2009; Hu et al., 2010). Comparison of archaeological and modern samples of cotton shows a startling amount of change in TE composition in *Gossypium herbaceum* over a short period of time (Fig. 2; Palmer et al., 2012). *Gossypium herbaceum*, from the Old World, is thought to be a very young species, speculated to be little older than the Holocene (Fryxell, 1979). This is supported by observations in our laboratory in which 10 out of 10 allele systems are unfixed

between this and its sister species, *G. arboretum*, in over 91 accessions tested (data unpublished). This contrasts with tetraploid cottons from the New World, which appear to have differentiated little from each other in over 1.5 million years (Senchina et al., 2003; Fig. 2). The cotton genus displays a pattern consistent with punctuated equilibrium, which has previously been linked to TE composition and turnover (Oliver and Greene, 2009, 2012). These apparently remarkable results require more work to explore cotton genome evolution directly. Tracing older cotton genomes would enable us to see the development of expansions over time and establish whether there is a reduction of diversity closer to the origin of speciation, or alternatively whether standing variation could better explain the Old World diploid species that does not occur in the New World tetraploids.

The ancient DNA evidence from cotton indicates that large amounts of small changeover can occur. We would predict that evolutionary change that occurs in this way that is adaptive would tend to affect traits in a polygenic fashion with no single locus usually carrying large effects. Therefore, when we think on a systems level, we would expect that gene networks would be affected at multiple points rather than single components of the network being causative of entire phenotypic traits. Ancient DNA can also be used to investigate genetic change at a systems level. Using the portion of the data set from the cotton study described above, which encompassed cotton gene fragments rather than TEs, we were able to identify 210 gene fragments that differed from public database entries. Of these, we could map 20 onto metabolic pathways and measure the distance between variants in terms of reaction nodes (Fig. 3). This analysis shows that 17 of the 20 variants fall in close proximity to each other in six metabolic clusters rather than a random pattern across the metabolic network. These clusters could be candidate regions to further study adaptive change in cotton.

This pattern of evolutionary adaptation of many genes under selection appears also to be an emergent feature of wild plant studies (Flowers et al., 2009; Hall et al., 2011; Keller et al., 2011). They also lead us to expect that gene networks and metabolic processes would be affected at multiple points. Interestingly, such a pattern has recently been observed in the adaptation of some dog lineages to a starchy diet in the human environment (Axelsson et al., 2013; Freedman et al., 2014). The simplicity of DNA binding sites involved in the regulation of gene expression and the consequent frequency with which they appear and disappear underlays the expectation of how gene networks effect rapid and complex adaptation to challenges (Alon, 2007). Therefore, we generally expect evolution to proceed without the loss of function of genes, when it proceeds at the complex level. The long-term plant–hominin co-evolution that ultimately leads to the appearance of a mixed domesticate–commensal plant community in the late stages of the Pleistocene might be expected to occur in this fashion, and methods to study it in plant genomes will likely require approaches that are able to detect weak selection per locus.

Subsequent to the emergence of the domesticate–commensal plant community, the rapid expansion of the human environment into higher latitudes with the spread of agriculture led to a contrasting pattern at the genetic level. As plants moved further north, the summer day lengths grew longer, resulting for wheat and barley in the threshold day length that induces flowering being reached sooner in the year, thereby shortening the growing season and reducing the plants' ability to produce sufficiently resourced grains. Rice, which detects shortening day lengths to flower in the autumn, reached its threshold later in the year at northerly latitudes and ran the risk of development continuing into the winter season. Instead of adjusting the expression of genes in the networks of the floral pathway to attune to these new latitudes as we might expect to have occurred naturally, we see irreversible loss of
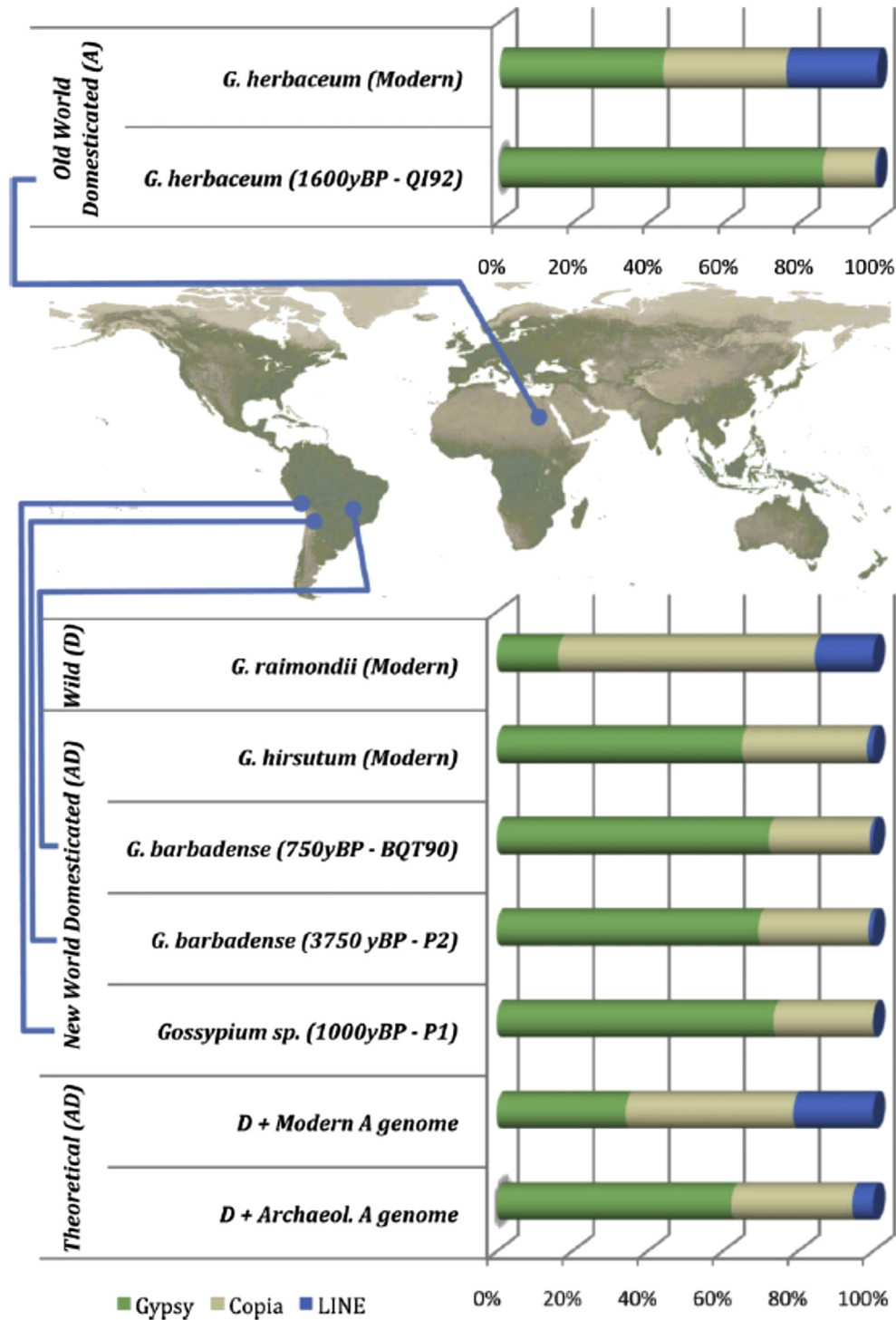
Figure 2. Genomic profiles of Gypsy-, Copia-, and LINE-type retrotransposons in modern and archaeobotanical cotton (*Gossypium* spp.). The dramatic change in the TE composition of the very young species *G. herbaceum* over a short period of time is evidence of large amounts of small change. In contrast, the very similar TE composition of the two *G. barbadense* samples indicates very little change despite the samples being separated by 2,000 miles and 3,000 years (from Palmer et al., 2012). yBP = years before present.

function mutations in the associated gene networks (reviewed in Fuller and Allaby, 2009). A loss of sensitivity to day length occurred in barley (Jones et al., 2008) and rice (Xue et al., 2008), negating the requirement for day length queues at all. Mutations in the vernalization genes remove the requirement for the experience of a winter season in order to induce flowering in cereals (Robson et al., 2001; Yan et al., 2004, 2006; Dubcovsky et al., 2005; Fu et al., 2005; Cockram et al., 2007), which helped plants move with the human

environment into northerly latitudes in which survival of the winter season would not have been assured. These adaptations of domesticated cereals to latitude appear crude, one-way, and simplistic relative to what we would expect of natural systems. In many cases, a single mutation achieves the phenotype rather than a number of mutations each contributing a small effect. Furthermore, these genotypes probably rose in frequency relatively rapidly given the rapid pace of the spread of agriculture (Colledge et al., 2005).
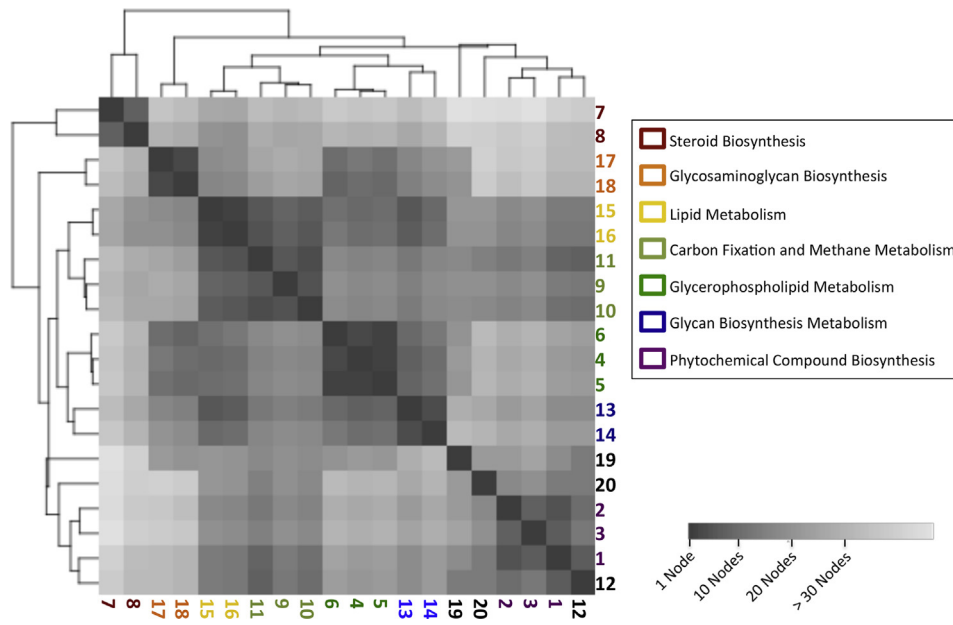
Figure 3. Cluster analysis of archaeological *Gossypium barbadense* read variants (Palmer et al., 2012) mapped to *Arabidopsis thaliana* metabolic pathways. Reads were mapped to the KEGG *A. thaliana* metabolic pathway. The number of major nodes between reads were used to create a distance metric between variants, which were then grouped by K-median clustering using the 'Pheatmap' package in R. Groupings have seven nodes or fewer between all points.

It is possible that these expansions and crude latitudinal adaptations represent the juxtaposition of adaptations of low complexity in complex environments, leading to the frequent collapse of agrarian societies. As such, the spread of agriculture may represent a period of disequilibrium in the long-term plant–hominin interaction, with a predisposed hominin side driving rapid change on the plant side. Currently available evidence suggests that such punctuations have been rare in plant–hominin co-evolution, although an interesting episode may have happened deep in the hominin lineage. During the cooling of the Pliocene 5.33–2.58 mya, predisposed plant forms (Christin et al., 2011, 2013) developed C4 metabolism and rapidly developed savannahs, dramatically changing the landscape and available food sources. In this case it may well have been the hominin lineage that was dragged across a selective gradient, and indeed this period and the Plio-Pleistocene boundary are associated with the rise of a large number of fundamental changes in hominin evolution, such as the appearance of stone tool technologies, increasing brain size, and a shift to a more C4-based diet (Aiello and Wheeler, 1995; Lee-Thorp and Sponheimer, 2006; Lee-Thorp et al., 2012). We might similarly expect to find signs of rapid adaptations of low complexity, perhaps gene network breakages, followed by frequent population collapse. Indeed, we do see the turnover of numerous hominin lineages in this period, including *Paranthropus robustus, P. boisei, Australopithecus afarensis, A. garhi, A. bahrelghazali, Homo rudolfensis,* and *H. habilis.* Although the evolution of C4 metabolism and the development of savannahs would create the sort of disequilibrium expected to drive the changes in human evolution that have been observed, it should be noted that the system could be more complex than a direct causal link, with other — as yet undiscovered — ecological factors involved. These punctuated episodes of rapid evolution and collapse are likely to be easier to detect at the genomic level, as they are predicted to be associated with strong signals of selection and the origination of pseudogenes. On the other hand, steady and complex plant–hominin co-evolution would be less readily visible and is predicted to be associated with very weak signatures of selection. While such signatures may not be detectable in extant genomes, the signatures of selection should be stronger in genomes closer in time to the onset of selection. This is possible with domesticate plants by sequencing archaeological genomes from a point in time significantly closer to the emergence of domesticated phenotypes. Obtaining archaeological plant genomes also negates a second confounding factor in studying plant adaptations: the occurrence of introgressions.

Both of these facets are excellently illustrated in the example of sorghum. Sorghum is characterized by five cultivated races that are thought to have progressively acquired qualities such as drought and pest resistance through repeated introgressions with the four wild races of the crop (Doggett, 1988, 1991). In this way, the domesticated crop was able to utilize adaptations of the different wild races to local environments. Until recently, efforts to detect signatures of selection in sorghum had proved largely fruitless (Hamblin et al., 2006), but extensive resequencing of 47 sorghum genomes has revealed some candidates (Mace et al., 2013). Domesticated forms of sorghum emerged relatively recently, around 6,000 years ago (Zohary et al., 2012). Archaeological remains of sorghum of excellent quality occur to almost half that age, which is allowing our group to carry out genome sequencing to test whether regions under selection become clearer in the past. These past genomes will also enable the reconstruction of the palimpsest of introgressions that went in to building up the modern plant today.

The expectation of complex evolution at a systems level is that most adaptive change will be at the regulatory level. Domesticated plants again fit this expectation with the vast majority of domestication syndrome traits for which the underlying genetic basis has been identified being regulatory in nature (Purugganan and Fuller, 2009). An important aspect of regulation is the action of RNA and epigenetic interactions such as the targeting of loci for methylation. There is little doubt that understanding how plants adapted to the human environment will require insights into these processes. RNA is highly prone to hydrolytic attack relative to DNA, partly because of its single stranded nature. However, while more labile than DNA, ancient RNA still occurs in useful quantities (Fordyce et al., 2013; Smith et al., 2014a). Furthermore, methylation can be detected in archaeological samples (Briggs et al., 2010; Llamas et al., 2012;

Smith et al., 2014b). Global methylation signals can indicate the general level of stress, and we recently detected elevated methylation levels in barley from an archaeological horizon associated with viral stress (Smith et al., 2014b). A major cause of methylation is due to the action of small interfering RNA (siRNA), RNA molecules of around 24 nucleotides that guide methyltransferase complexes to specific sequences of DNA. In the case of the barley it was also possible to detect candidate putative siRNA interference associated with the targeted methylation of a disease-associated locus (Smith et al., 2014b). Therefore, ancient DNA technology has progressed to the point at which the methylation states of loci across genomes can be tracked directly through time.

Conclusion

The largely archaeology-led reinterpretation of the evolution of domestication has led to exploration of new genetic models, which are testable through ancient DNA in particular. As a consequence, the question has moved from whether plant domestication was fast or slow, single or multiple origin, to one that addresses why domestication was so slow and similar to natural selection in terms of the selection pressures involved. The notion that the evolution of domestication is something that is like natural selection but much faster is traceable to Darwin's original thesis (Darwin, 1859), where he used it extensively to demonstrate the feasibility of modification by descent. However, it is apparent that the evolution of domestication is a better vehicle for explaining natural selection than even Darwin might have imagined because it actually is a case of natural selection (Larson et al., 2014). The removal of the requirement of an artificial selection explanation also removes the requirement of the components of human invention and revolution that have previously been applied to a scenario in which plants were the passive recipients of artificial selection. Instead we are left with a coherent picture in which a broader plant community adapted to human processing of the environment around them. This human engagement in processing stretches back into the Pliocene, where new energy-rich foodstuffs were exploited through the utilization of tools for the first time, for instance through digging up root tubers (Hillman and Wollstonecroft, 2014).

A picture of hominin–plant coevolution is consequently becoming more apparent, for which models predict a complex evolution for the most part that is expected to proceed slowly and spread across many loci. The evidence that we have seen so far from ancient DNA would appear to support this, and NGS approaches to track archaeological genomes directly over time will further clarify this process.

In this scenario, however, movements of one or other half of the hominin–plant contract have at times caused the other to be dragged rapidly across selective gradients. This has led to rapid, low complexity adaptation in complex environments leading to the extinction of lineages. Under this model we can map examples, such as the rise of large-brained hominins and the fall of many other lineages as respondents to major shifts in the rise of savannah plants, and the adaptation of many plants to northern latitudes as respondents to the spread of agricultural societies. By considering these processes as part of the same co-evolutionary continuum, understanding one part of the process can be expected to inform the other.

Acknowledgements

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