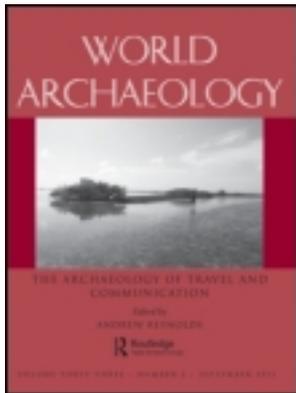


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Cultivation and domestication had multiple origins: arguments against the core area hypothesis for the origins of agriculture in the Near East

Dorian Q Fuller^a, George Willcox^b & Robin G. Allaby^c

^a Institute of Archaeology, University College London E-mail:
d.fuller@ucl.ac.uk

^b CNRS

^c University of Warwick

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Cultivation and domestication had multiple origins: arguments against the core area hypothesis for the origins of agriculture in the Near East

Dorian Q Fuller, George Willcox and Robin G. Allaby

Abstract

This paper debates claims that plant domestication occurred rapidly in a single restricted sub-section of the Near Eastern Fertile Crescent. Instead we argue for numerous parallel processes of domestication across the region in the Early Holocene. While a previous generation of genetic results seemed to support a single 'core area', the accumulation of genetic evidence and refinements in methods undermine this, pointing increasingly towards multiple geographical origins. We stress that it is important to recognize that modern germplasm collections are an imperfect sample of the diversity of wild and cultivated populations of the past, which included some extinct lineages. We briefly synthesize the accumulated data from archaeobotany, defending the reliability of archaeological science to inform us about the past plant populations used by people. These data indicate an extended period of pre-domestication cultivation of at least a millennium and the slow evolution of morphological domestication adaptations in crop plants. The appearance of early cultivars and domesticates was spread piecemeal around the Near East, and a whole crop package is not evident. The 'core area' claimed by some authors has no better claim for primacy or completeness in comparison to other parts of the Near East. Evidence from zooarchaeology similarly points towards a diffuse appearance of various domesticated animals. The 'non-centric' appearance of domesticates from the Near East is therefore similar to the emerging evidence from many other regions of the world where plants were domesticated. We develop a hypothesis of why this should be expected given that anatomically modern human ancestors shared practices of vegetation management and planting, the necessary background knowledge for cultivation. Cultivation then was not a rare discovery but was a strategic and systematic shift in economies. The question then becomes why it was developed in the particular regions and periods where it appeared.

Keywords

Neolithic; agriculture; centres of origin; archaeobotany; palaeoethnobotany; wild progenitors.

Introduction: beyond an Edenic oasis

The archaeological quest for agricultural origins has long sought to pinpoint a key place where it all began. In the 1980s, when the best-known sequence was that of the Southern Levant, explanatory models for the beginnings of agriculture in the West Asia focused on this region and the transition from the Natufian to the Pre-Pottery Neolithic (e.g. Henry 1989). This replaced an earlier interest in the hilly flanks of the Zagros and Taurus mountains where ecological models had been developed to explain domestication in the 1960s and 1970s (e.g. Bender 1975). However, by the end of the 1990s the centre of origin had shifted again, this time to southeast Turkey, where the upper Euphrates river comes closest to the Karadag mountains. Lev-Yadun et al. (2000) declared this as the ‘core area’ for agricultural origins. This core area was defined also by the overlap of modern wild progenitor ranges of emmer wheat, einkorn wheat, barley, pea, lentil, chickpea and bitter vetch in this same region (Fig. 1). Kozłowski and Aurenche (2005) have taken on this singular area of domestication as their ‘golden triangle’ (cf. Asouti 2006: 95). On archaeological grounds, Bar-Yosef (2003) postulated an adjacent and overlapping core on the Upper to Middle Euphrates.

Nevertheless, there has been a growing body of studies that do not fit with any one core area, but suggest a dispersed group of parallel processes (Allaby et al. 2010; Asouti 2010; Belfer-Cohen and Goring Morris 2010; Brown et al. 2009; Fuller 2007, 2008; Nesbitt 2004;

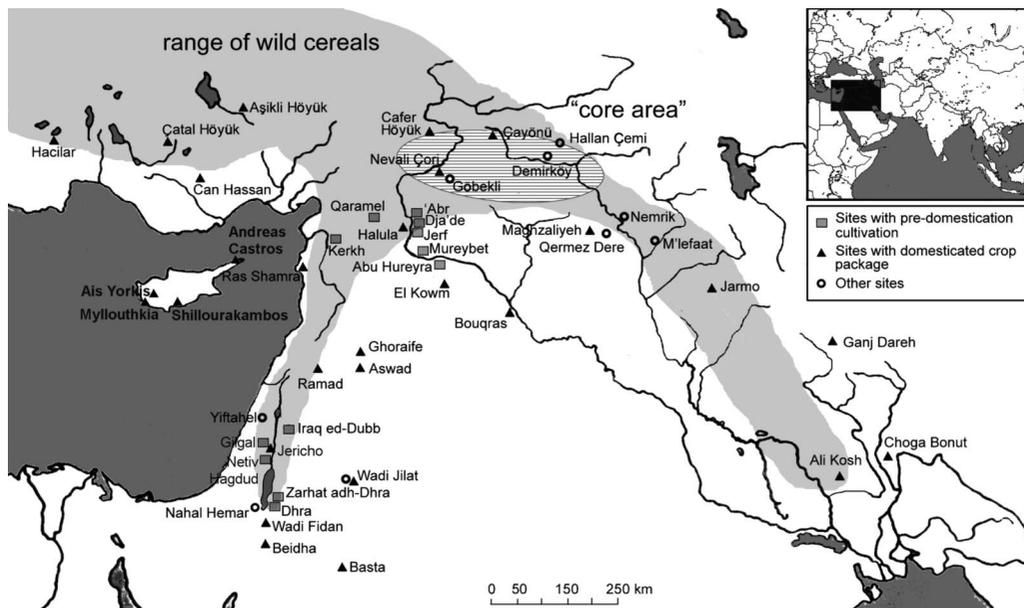


Figure 1 Map of the Near Eastern early Neolithic sites with archaeobotanical evidence, in relation to the general distribution of wild cereals and the hypothetical Core Area, based on the overlap of a selection of progenitors, including *Cicer arietinum*. Sites are differentiated into those with inferred pre-domestication cultivation (Table 1) and those with an established package of domesticates (presence of at least two confirmed morphological domesticates and at least a third domesticate/semi-domesticated, based on Table 1).

Willcox 2005; Zeder 2009). While some have declared a paradigm shift to multiple and protracted origins (e.g. Fuller 2010), there remains the contention that domestication happened just once in the Near East in a contracted area over a fairly short time of at most a few centuries (Abbo et al. 2010, 2011; Honne and Heun 2009). While Haldersen et al. (2011) are careful to consider only one-grained einkorn, they argue explicitly for a rapid, single domestication event, implying that archaeobotanical evidence is inadequate and flawed as a means of studying domestication. In the present paper, we will debate the existence of a single core of domestication in the Near East and defend the importance of systematically collected and studied archaeobotanical evidence for studying the origins of agriculture. A diffuse and protracted process of origins in Southwest Asia is representative of recurrent global processes: evidence from other continents also suggests multiple locales and paces of domestication. While this implies that there was no one prime mover globally that caused humans to farm, we hypothesize that it is symptomatic of shared, ancestral human predilections towards landscape management.

Evolving genetic approaches to pinpointing domestication

As molecular genetic approaches to organismal diversity became increasingly available, it seemed obvious that this would provide a new tool for definitively identifying where species were domesticated. Genes after all are the products of evolutionary history, and should allow for inferring the phylogenetic pattern of that history. It would seem obvious then to ask whether a crop was monophyletic or polyphyletic with regard to its wild progenitor, and to use these patterns to infer where domestication had occurred. Unfortunately, this intuitive inference hides serious flaws, which have become increasingly apparent as both the total amount of genetic data has increased and as the mathematics (bioinformatics) of dealing with these data has improved. Genetic data are reflections not merely of phylogenetic history but also of the processes of population genetics: drift, selection, linkage, lineage extinction and lineage sorting. In 1997, Heun et al. (1997) published the first major molecular genetic study of domestication, pinpointing the *modern* wild population of einkorn of the Karaċadag mountains as the ancestors from which einkorn had been domesticated *in the Neolithic*. This study became a model (AFLP ‘finger-printing’ analyzed with Neighbour-Joining Trees) followed in numerous other studies, on crops from barley (Badr et al. 2000), to potato (Spooner et al. 2005), coffee (Anthony et al. 2002) and vanilla (Bory et al. 2008). This extended to the more general model of genome wide markers (GWM), such as microsatellites, for instance on maize (Matsuoka et al. 2002), cassava (Olsen et al. 2001) and emmer (Özkan et al. 2011), which are subject to the same pitfalls. Despite its flawed assumptions, the conclusion that all einkorn derived from a single rapid domestication event in the Karaċadag mountains remains a persistent factoid (e.g. Abbo et al. 2011; Charmet 2011; Haldersen et al. 2011), which continues to bias interpretations of Near Eastern archaeological evidence towards locating a single source of agriculture in Southeast Turkey.

There are problems with the assumption that modern wild and cultivated populations represent all those of the past, assuming that there have been no local extinctions, despite millennia of climatic changes and human impacts, and assuming that no evolution – by adaptation or by genetic drift – might have altered the picture in modern wild populations.

Even if this objection could be set aside as insignificant, the method of analysis assumed that the history since domestication had been entirely tree-like, with divergence between populations and never hybridization. Even in a selfing species such as wheat, in which cross pollination may be as low as 1–2 per cent, there was gene flow and hybridization. Indeed hybridizations have been very important from an agricultural point of view, providing for polyploidy, including the evolution of wild emmer (before it was ever domesticated) and hexaploid wheats such as bread wheat and spelt which resulted from hybridizations after emmer had been domesticated (Charmet 2011; Zohary and Hopf 2000). Hybridization events have been important in the evolution of many crops, from bananas (De Langhe and De Maret 1999; Simmonds 1962), to Asian rice (Fuller et al. 2010a; McNally et al. 2009). Simulated data showed that the methods used by Heun et al. (1997) would almost always infer a single origin even when more than one origin was simulated (Allaby et al. 2008, 2010). In other words, that type of data and analytical method was unable to detect multiple domestication events. Meanwhile other genetic studies, using other systems, provided increasingly heterogeneous results, suggesting the capture of multiple wild genotypes with domestication, which seems to imply two or more domestications in einkorn (Kilian et al. 2007), emmer (Brown et al. 2006; Özkan et al. 2011), barley (Azhaguvel and Komatsuda 2007; Jones et al. 2008; Morrell and Clegg 2007; Saisho and Purugganan 2007), pea (Kosterin and Bogdanova 2008), lentil (Mayer and Soltis 1994). Older genetic proxies implied perhaps two domestications of bitter vetch (Ladizinsky and Van Oss 1984).

The accumulation of archaeobotanical evidence also highlights the inadequacy of relying only on the genetics of modern plant collections in order to infer the history of domestication. Archaeobotanists now recognize several morphological cereal types no longer present among modern cultivated germplasm. These archaeological taxa imply additional domestication events and the dispersal of lost crop lineages. Among these were two-grained einkorn, documented as a wild resource in the Epipalaeolithic, as an inferred cultivar on upper Euphrates sites such as Jerf el Ahmer, Mureybet and Dja'de (Willcox and Fornite 1999; Willcox et al. 2008), and later as a domesticated cereal at many LPPNB sites from Anatolia to the Jordan (see Table 1, Fig. 2). This species also spread to Neolithic Europe, where it became especially prominent in the Neolithic of Southeast and central Europe (Kreuz and Boenke 2002). While it seems to disappear from the archaeological record in its Syrian homeland by *c.* 5000 BC (Van Zeist 1999), it persists in Europe until the later Bronze Age, becoming extinct perhaps around 1000 BC (Köhler-Schneider 2003).

A similar story can now be sketched for a striate emmeroid wheat, the so-called 'new type glume wheat', which is known from Anatolia, Eastern and Central Europe and Turkmenistan (Charles and Bogaard 2010; Jones et al. 2000; Köhler-Schneider 2003), and similarly disappeared from European agriculture during the Bronze Age. Early ancient DNA work on the wheats from Bronze Age Assiros, Greece, identified the presence of G-genomes (Brown et al. 1998), i.e. AAGG wheat like that in the relict *Triticum timopheevi* of Georgia/Ukraine, rather than the AABB genomic make-up of standard emmer. This raises the likelihood that the striate emmeroid was a *timopheevi*-type of glume wheat. However, the extremely restricted distribution of modern *Triticum timopheevi* means that the genetic diversity of the ancient spread of this wheat through Europe and eastwards to Central Asia is unlikely to be covered in genetic sampling focused only on modern germplasm

Table 1 Tally of crops/potential cultivars.

| | <i>Cal. BC mode (range)</i> | <i>Triticum monococcum</i> 2-gr | <i>Secale sp.</i> | <i>Triticum monococcum, I-gr</i> | <i>Triticum dicoccoides</i> | <i>Triticum diococcum vulgare </i> | <i>Hordeum spontaneum</i> | <i>Linum usitatissimum</i> | <i>Lens culinaris orientalis</i> | <i>Pisum sativum</i> | <i>Cicer arietinum</i> | <i>Vicia ervilia</i> | <i>Vicia faba</i> | <i>Tally</i> |
|------------------------|---------------------------------|--|-----------------------|--|---------------------------------|---|-------------------------------|--------------------------------|---|--------------------------|----------------------------|--------------------------|-----------------------|--------------|
| <i>Southern Levant</i> | | | | | | | | | | | | | | |
| Iraq ed-Dubb | 9300 (9700–8800) | ? | | ? | x ^{wd} | x ^{wd} | x ^{wd} | x | x ^{wd} | x ^{wd} | ? | | x | 3 |
| Gilgal I | 9300 (9400–9100) | | | | x [?] | x [?] | x | | | | | | | 2 |
| Netiv Hagdud | 9200 (9300–8850) | | | | x | x | x | | x | | | x | | 4 |
| Zahrat adh-Dhra' 2 | 8800 (9150–8650) | | | | x ^{wd} | x ^{wd} | x ^{wd} | | x | ? | | x | | 3 |
| Jericho I (PPNA) | 8700 (9150–8350) | | | x ^{wd} | x ^{wd} | x ^{wd} | x ^{wd} | x | x ^{wd} | x ^{wd} | ? | | x | 6 |
| Tell Aswad | 8400 (8700–8200) | | | | x ^{wd} | x ^{wd} | x ^{wd} | | x ^D | | | x | | 4 (1) |
| Beidha | 7900 (8300–7550) | x | | | x ^{wd} | x ^{wd} | x ^{wd} | | x ^D | x ^D | x ^D | x | | 5 (2) |
| Wadi Jilat 7 | 7800 (8200–7500) | x ^{wd} | | x ^{wd} | x ^{wd} | x ^{wd} | x ^{wd} | | | | ? | | | 4 |
| Yiftahel | 7800 (8200–7650) | | | | x ^{wd} | x ^{wd} | x ^{wd} | | x ^D | | | | x | 1 (1) |
| Jericho II (PPNB') | 7700 (8200–7500) | | | x ^D | x ^D | x ^D | x ^D | x | x ^D | x ^D | ? | | x | 7 (5) |
| Nahal Hemar | 7700 (8000–7050) | | | | x ^{wd} | x ^{wd} | x ^{wd} | | | | | | | 2 (1) |
| Ghoraife | 7500 (7800–7050) | | | x ^D | x ^D | x ^D | x ^D | x | x ^D | x ^D | | x | | 7 (5) |
| Basta | 7400 (7550–7050) | x ^D | | x ^D | x ^D | x ^D | x ^D | | x ^D | x ^D | | x | | 7 (6) |
| Ain Ghazal | 7200 (8300–6600) | | | | x ^D | x ^D | x ^D | x | x ^D | x ^D | | x ^D | x | 7 (5) |
| Tell Ramad | 7100 (7300–6650) | x [?] | | x ^D | x ^D | x ^D | x ^D | x | x ^D | x ^D | | | | 8 (6) |
| Wadi Fidan A | 7100 (7300–6750) | x ^D | | ? | x ^D | x ^D | x ^D | x | x ^D | x ^D | | | | 3 (3) |
| Wadi Jilat 13 | 6700 (7050–6600) | x ^D | | x ^D | x ^D | x ^D | x ^{wd} | | | | | | | 4 (3) |

(continued)

Table 1 (Continued)

| | Cal. BC mode (range) | Triticum monococcum 2-gr | Secale monococcum sp. | Triticum I-gr monococcum, | Triticum dicoccoides | Hordeum vulgare/ spontaneum | Linum usitatissimum | Lens culinaris/ orientalis | Pisum sativum | Cicer arietinum | Vicia ervilia | Vicia faba | Tally |
|---------------------------------|-------------------------|--------------------------------|-----------------------------|---------------------------------|-------------------------|-----------------------------------|------------------------|----------------------------------|------------------|--------------------|------------------|---------------|-------|
| <i>'Core Area'</i> | | | | | | | | | | | | | |
| Hallan Çemi | 9500 (9700–9300) | x | | | | x | | x | ? | | x | | 4 |
| Demirköy | 9350 (9450–9300) | | | | x | x | | x | | | | | 3 |
| Göbekli Tepe | 8800 (9200–8600) | x | ? | | | x | | | | | | | 2 |
| Çayönü (RP, GP,Ch,H) | 8300 (8700–8000) | x ^{wd} | | x ^{wd} | x ^{wd} | x | x | x | x | x | x | x | 10 |
| Nevali Çori | 8300 (8600–7950) | x ^{wd} | | x ^{wd} | x | x | | x | x ^D | ? | x | x | 8 (1) |
| Cafer Höyük | 8100 (8300–7800) | x | | x ^D | x ^D | x | | x ^D | x | | x | x | 9 (4) |
| IX-XIII | | | | | | | | | | | | | |
| Cafer Höyük III-VIII | 7600 (8300–7450) | | | x ^D | x ^D | x ^D | | x ^D | | | | | 4 (4) |
| <i>Northern Levant/Anatolia</i> | | | | | | | | | | | | | |
| Abu Hureyra I | 10,600 (11,150–10,450) | x | x ^{wd} | | | | x | x | | | x | | 5 |
| Tell Qaramel | 9700 (10,300–8850) | | | x | | x | | x | | | x | | 5 |
| Mureybet I-III | 9400 (9700–8500) | x | x | | | x | x | x | | | x | | 6 |
| Tell 'Abr 3 | 9350 (9500–9200) | x | | | | x | | x | | | | | 4 |
| Jerf el Ahmar | 9300 (9450–8700) | x ^{wd} | x | | | x ^{wd} | | x | x | | x | | 7 |
| Dja'de | 8500 (8700–8250) | x ^{wd} | x | x | | x ^{wd} | | x | x | | x | | 9 |
| Mureybet IV | 8400 (8750–7950) | x ^D | | | | x | | x | | x ^D | ? | | 5 |
| Tell el-Kerkh | 8400 (8550–8300) | ? | | x ^{wd?} | x | x | | x | | | x | x | 7 (1) |
| Hacılar | 7800 (8200–7550) | | | x ^D | x ^D | x ^D | | x ^D | | | | | 4 (4) |
| Tell Halula | 7650 (7800–7300) | | | x ^D | x ^D | x ^D | | x ^D | | | x | x | 6 (3) |
| Ağıkh Höyük | 7600 (7800–7500) | x | | x ^D | x ^D | x ^D | | x | x ^D | ? | x | x | 6 (4) |
| Can Hasan III | 7600 (7800–6500) | | x ^D | x ^D | x ^D | x ^D | | x ^D | x ^D | | x | | 7 (5) |
| Abu Hureyra 2A-C | 7400 (7800–7000) | x ^D | x ^D | x ^D | x ^D | x ^D | x | x ^D | ? | x ^D | ? | x | 8 (6) |
| Ras Shamra | 7200 (7600–6000) | ? | | x ^D | x ^D | x ^D | | x ^D | | | | | 6 (5) |
| Tell Bouqras | 7100 (7500–6300) | | | x ^D | x ^D | x ^D | x | x ^D | | | | | 6 (5) |
| Çatalhöyük East | 6900 (7100–6400) | ? | | x ^D | x ^D | x ^D | | x ^D | | | x | | 7 (6) |
| El Kowm II | 6600 (7100–6350) | x ^D | x ^D | x ^D | x ^D | x ^D | | x ^D | | | x | | 5 (4) |

(continued)

Table 1 (Continued)

| | Cal. BC mode (range) | Triticum monococcum | | Triticum dicoccoides | Hordeum | | Lens | | Pisum sativum | Cicer arietinum | Vicia ervilia | Vicia faba | Tally |
|---------------------------------|-------------------------|---------------------|-----------------|-------------------------|-----------------|------------|-----------------|------------|------------------|--------------------|------------------|---------------|-------|
| | | 2-gr | 1-gr | | vulgare/ | spontaneum | culinaris/ | orientalis | | | | | |
| <i>Eastern Fertile Crescent</i> | | | | | | | | | | | | | |
| Qermez Dere | 9200 (10,100–8800) | | | | x | | x | | | | x | | 3 |
| M'lefaat | 9200 (9500–8800) | | ? | | x | | x | | | | x | | 3 |
| Nemrik | 8400 (10,200–8200) | | | | x ^D | | x | | x | | | | 2 |
| Ganj Dareh | 8100 (8250–7850) | | | x ^D | x ^D | | x ^{wd} | | x | | | | 3 (1) |
| Tepe Abdul Hosein | 8000 (8300–7800) | | | x ^D | x ^D | | x ^D | | x | | | | 3 (3) |
| Jarmo | 7700 (8000–7400) | | x ^{wd} | x ^{wd} | x ^{wd} | | x ^D | | x ^D | | | | 5 (2) |
| Ali Kosh (B M ph.) | 7300 (7650–6800) | | x ^D | x ^{wd} | x ^D | | x ^D | x | | | | | 4 (2) |
| Chogha Bonut | 7250 (7600–6900) | | x ^D | x ^D | x ^D | | x ^D | | | | | | 4 (4) |
| Tell Maghazaliyeh | 6700 (7100–6300) | | x ^D | x ^D | x ^D | | x ^D | x | | | | | 5 (4) |

Notes:

x = present.

No superscript means wild/presumed wild; superscript D = domesticated, wd = 'semi-domesticated'.

Tally indicates numbers of crops present with confirmed domesticated counts in parentheses.

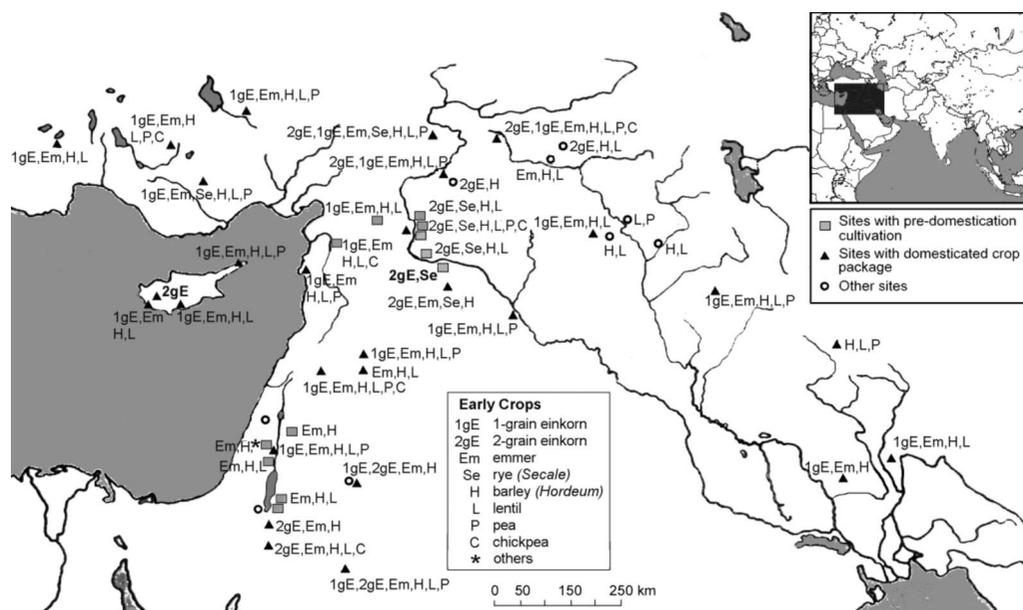


Figure 2 Map of the Near Eastern early Neolithic sites (same as Figure 1), indicating the distribution of early crops (or wild progenitors) across sites and regions.

collections. Similar examples could be cited from animals, such as pigs (Larson 2011). Thus we must conclude that modern genetic data, even with the best of modern methodologies, can at best provide a partial evolutionary history of crops.

Archaeobotany can identify cultivation and domestication

Archaeobotanical specialists working with Near Eastern material have come to recognize that domestication was a prolonged process. Hillman and Davis (1990) had hypothesized that domestication could have been quite rapid (twenty to 100 years) based on extrapolation of modern experiments, and an assumption of shifting cultivation, but the archaeological data to test this rapidity did not become available in quantity until the past few years (see Allaby et al. 2010; Fuller 2007; Tanno and Willcox 2006). Two lines of archaeobotanical evidence, however, argue against rapid domestication: evidence for pre-domestication cultivation and the gradual replacement of wild-type morphological traits by domesticated morphological traits over several millennia.

Pre-domestication cultivation refers to evidence for either the emergence of an arable weed flora or the presence of substantial stores of a plausible crop beyond what might be expected to be gathered wild. Pre-domestication cultivation has been inferred specifically at some ten sites from both the southern and northern Levant (Colledge 2001; Edwards et al. 2004; Harris 1998; Hillman et al. 2001; Van Zeist and De Roller 1992; Weiss et al. 2006; Willcox 2011; Willcox et al. 2008), although it might be suggested to be present at still more. These sites date predominantly to the tenth millennium BC (the PPNA) and the

Early PPNB up to *c.* 8200 BC (Fig. 3). Unlike the rapid 100-year domestication still postulated by some (e.g. Abbo et al. 2010; Haldersen et al. 2011), evidence of pre-domestication cultivation is focused on at least 1500 years. Weiss et al. (2006) argued in the absence of a weed flora that the substantial quantities of wild-type cereals, including emmer wheat, barley, lentils and an oat (*Avena*) that PPNA occupations in the lower Jordan Valley indicated that cultivation was practiced for perhaps a millennium before domestication traits first appeared. Melamed et al. (2008) established the likelihood that *Vicia peregrina* was also cultivated and consumed in this region, although this species has not persisted as a crop. Kislev et al. (2006) inferred that figs may have been vegetatively propagated. Although this interpretation can be criticized (e.g. Denham 2007), it is nevertheless striking that figs have become a recurrent find on other early cultivation sites from the Early PPNB (e.g. Willcox et al. 2008). Elsewhere, the association of morphologically wild cereal remains, usually indicated by wild type rachises, together with substantial quantities of taxa that are most common in recent times as arable weeds,

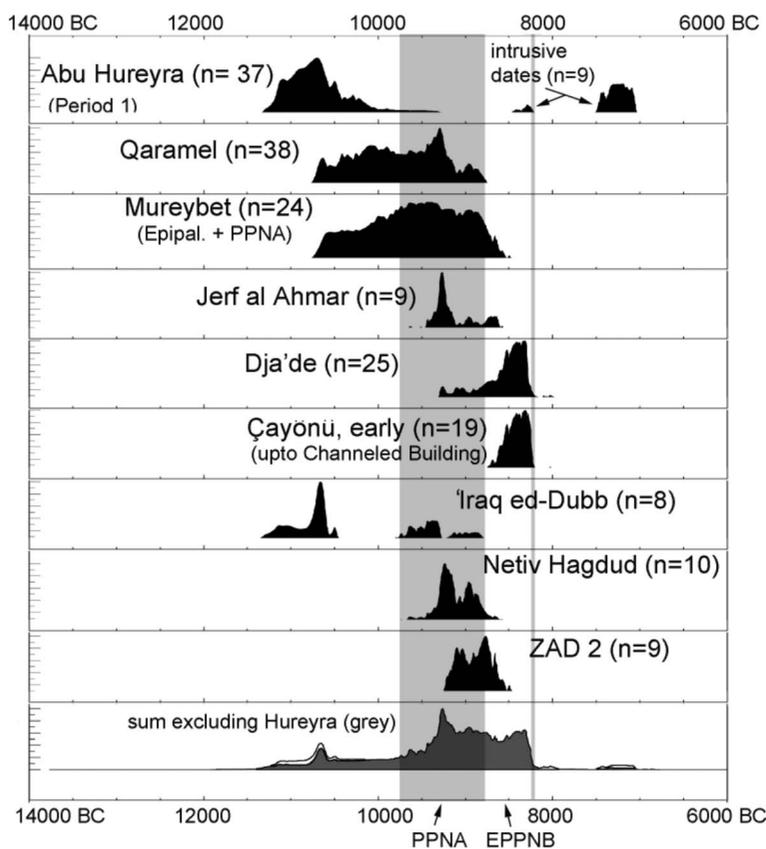


Figure 3 The summed calibration probability of radiocarbon dates associated with nine sites/levels with inferred evidence for pre-domestication cultivation. At the bottom of the chart the total sum for all is shown. Note the clear modal probabilities on the PPNA and Early PPNB (9700–8200 BC). Calibration was performed with OxCal 3.10 (Bronk Ramsey 2005) using the revised IntCal09 calibration curve (Reimer et al. 2009). Raw dates from on-line PPND (Benz 2010).

suggests the creation of a new arable habitat. This has been approached statistically (Colledge 1998, 2001), as progressive assemblage change (Hillman et al. 2001) and cautiously by excluding any potential gathered food plants (Willcox 2011; Willcox et al. 2008). The persistence of many of these same taxa as weeds of cultivation into later agricultural periods and their co-dispersal into Europe with the first agriculture (Colledge et al. 2004; Coward et al. 2008) all point to the origins of many agricultural weeds before the morphological domestication of cereals.

The delayed appearance and slow rise to dominance of domestication traits has been documented only recently in wheat and barley (Fuller 2007; Tanno and Willcox 2006, 2011), and the data parallel those on rice (Fuller et al. 2009). Time series data of cereal shattering indicate a slow rate of change, taking something like 3000 years to shift from fully shattering to non-shattering (Fuller et al. 2010b; Purugganan and Fuller 2011). Grain size evolution seems to potentially occur independently, starting earlier in wheat and barley (Fuller 2007; Willcox 2004) and later in pearl millet (Manning et al. 2011) than non-shattering. While some of this seed size change may be induced by improved environmental conditions of cultivation, i.e. phenotypic plasticity (Willcox 2004), the longer-term trend of change for the first 3000–4000 years of cultivation, and known genes affecting grain size, selected in domesticated populations, point to an evolutionary process (Fuller and Allaby 2009; Fuller et al. 2010b; Gegas et al. 2010).

Haldersen et al. (2011) have attempted to dismiss these patterns in the case of einkorn by suggesting that wild einkorn came into assemblages as a weed of rapidly domesticated einkorn. Setting aside that this fails to account for the strikingly parallel rates of change in barley and rice, or the gradual change in grain size, or to counter models of how human practices should be expected to select for slow domestication (Fuller et al. 2010b), this inference would imply that the decrease in wild einkorn over time (from the earlier to later levels at Cafer Höyük, for example) was due to the gradual elimination of the weed species. However, if a change in cultivation practice were to eliminate a weed, we would expect it to be quite sudden. It seems hard to imagine how weed einkorn would have been eliminated given its morphological similarity to domestic einkorn. The archaeological record of change in crop plant morphology seems best interpreted as evolution of cultivated populations.

The appearance of domesticates: core area or mosaic?

Here we provide a detailed archaeobotanical assessment of the evidence for the ‘core area’ in comparison to other parts of the Near East. In Table 1 the presence/absence of crops is summarized, and whether morphological domestication traits are evident. Domesticated crops are taken to include cereals in which non-shattering rachises are in the majority, or where seed size (in cereals, pea, lentil) of the measured population is significantly larger than in wild populations or measured populations at the earliest sites. Mixed wild/domestic ‘semi-domesticate’ status is given to assemblages in which non-shattering cereal rachises account for 10–50 per cent (a minority, but more than can be expected in the wild for this deleterious mutation) or in which grain size shows some increase in average over the earliest assemblages but is not as large as or significantly different from later

assemblages (details of these domestication data can be found in the on-line supplement to Purugganan and Fuller 2011). Because not all assemblages have been documented and published to the same detail, these criteria will tend to err on the side of assuming wild until proven domesticated.

All regions of the fertile crescent show a pattern of an increasing range of probable crops over time and a delayed but increasing range of confirmed domesticates (see Table 1). A few earlier sites in the 'core' region such as Hallan Çemi and Demerköy have evidence for fewer wild progenitors than are found on equally early sites elsewhere. Furthermore, the number of species that have domesticated morphology or even intermediate 'semi-domesticate' status are few, semi-domesticated einkorn and emmer at Çayönü and semi-domesticated einkorn and domestic-size peas at Nevalı Çori. By contrast peas remain in wild size range at Cafer Höyük, while lentils appear domesticated, as do cereals based on rising frequencies (but not dominance) of non-shattering rachises.

Early cultivation in the Near East appears to have been multi-focal and piecemeal. In Figure 2, we have indicated the early presence of crops, inferred to be cultivated, across different parts of the Near East. From this it can be seen that no site or region in the PPNA or Early PPNB can claim to represent the Near Eastern founder crops. Instead different local selections seem to be in operation. Some lost crops, such as rye and two-grained einkorn have surprisingly wide distributions. We infer from this that different local wild populations were brought into cultivation and in multiple contexts were selected for domestication adaptations. The situation in Cyprus is striking in that no single pattern of cereals cultivated is common to all the sites, and cereals arrived on Cyprus before they were morphologically domesticated on the mainland (Lucas et al. 2011).

The ultimate agricultural economies that came together by the Late Pre-Pottery Neolithic included livestock as well as crops. The appearance of livestock also appears similarly diffuse (Conolly et al. 2011; Vigne 2008; 2011; Zeder 2008). In Table 2, we have summarized the earliest reports of domesticated animals around the Near East. Only at Çayönü, which has one of the longest sequences, is there possible evidence for all four domesticated animals quite early, although the dominance of domesticated sheep and goat appears later than early evidence for pig and cattle herding (Hongo et al. 2005, 2009). Nevertheless, domestic fauna appeared in subsets, in part tailored to local ecological and economic adaptations, but also probably due to multiple processes of taming and breeding. Interestingly, although all four species are introduced to Cyprus at an early date, some appear to have been managed as wild populations for hunting while others were herded (Vigne 2011). Because archaeozoological evidence is produced by very different conditions from archaeobotanical remains, the similar patterns suggest that both datasets are symptomatic of past economic realities. While some might contend that archaeobotanical evidence is inherently fragmentary and inadequate, as implied by Halderson et al. (2011), the strength of this pattern across plant and animal assemblages and numerous researchers is clear. It is of added significance that the appearance of livestock correlates with the period that saw greater commitment to crops and evolution towards plant domestication traits (Fuller et al. 2010b), since it has been argued that herding and cultivation were integrated in small-scale intensive systems, rather than the shifting fields postulated by Hillman and Davis (1990), and it was such systems that became an expansive economic system that later spread to Europe (Bogaard 2005).

Table 2 Earliest reports of animal domestication in the Fertile Crescent.

| Site | Period | Goat | Sheep | Cattle | Pig | References |
|--|---------------------------------|----------------------------------|----------------------------------|---------------------------------------|--------------------------|---|
| <i>Anatolia</i> | | | | | | |
| Asikli Hoyuk | MPPNB (7800–7500 BC) | Age prof.; size | Age prof.; size | | | Arbuckle et al. 2008 |
| <i>'Core Area'/Northern Fertile Crescent</i> | | | | | | |
| Cayonu | EPPNB (Grill) (8400–8200 BC) | Later: size decrease (M PPNB) | Later: size decrease (M PPNB) | Age prof.; stable isotopes | Age prof.; size decrease | Hongo et al. 2005, 2009 |
| Nevali Cori | E/M. PPNB (8600–7900 BC) | Size; stable isotopes | Size; stable isotopes | | | Lösch et al. 2006; Peters et al. 2005 |
| Cafer Hoyuk | MPPNB (8300–7400 BC) | Size | Size | | | Conolly et al. 2011; Legge 1996 |
| <i>Cyprus</i> | | | | | | |
| Shillouro-kambos | E/MPPNB (8400–8000 BC) | Ex-wild area | Ex-wild area | Ex-wild area | Ex-wild area | Vigne 2011; Vigne et al. 1999 |
| <i>Eastern Fertile Crescent</i> | | | | | | |
| Ganj Dareh | MPPNB (8200–7800 BC) | Age prof. | | | | Zeder 2005; Zeder and Hesse 1999 |
| <i>Middle Euphrates/Northern Levant</i> | | | | | | |
| D'jade | EPPNB (8700–8200 BC) | | | Decreased dimorphism; T-haplo. (aDNA) | | Edwards et al. 2007; Helmer et al. 2005 |
| Abu Hureyra | M/L. PPNB (7800–7000 BC) | Ex-wild area | Ex-wild area | | | Legge 1996 |
| Tell Halulua | M. PPNB (7800–7300 BC) | Ex-wild area | Ex-wild area | | Ex-wild area | Helmer and Gourichon 2008; Helmer et al. 2005 |

(continued)

Table 2 (Continued)

| Site | Period | Goat | Sheep | Cattle | Pig | References |
|------------------------|-----------------------------|-----------------|-------|--------------|--------------|--|
| Sabi Abyad II | M/L. PPNB (7700–6700 BC) | | | | Ex-wild area | Helmer and Gourichon 2008 |
| <i>Southern Levant</i> | | | | | | |
| Tell Aswad | E/M. PPNB (8700–7500 BC) | Size | | Ex-wild area | Ex-wild area | Helmer and Gourichon 2008, in press |
| | M.PPNB (8300–7550 BC) | Age prof., size | | | | Legge 1996 |
| Beidha | M/L. PPNB (8300–6600 BC) | Age prof., size | | | | Legge 1996 |
| Ain Ghazal | | | | | | |

Notes:

Under the column of each taxon the line(s) of evidence for inferring domestication are indicated.

Age prof. = age profile; stable isotopes = shift in diet from expected wild signature indicated in stable N and C isotopes; ex-wild area = finds outside predicted wild range; T-haplo. = presence of domestic lineage haplogroup in ancient DNA.

The picture in the faunal and floral records is congruent with recent syntheses of the wider archaeological evidence. For example, Belfer-Cohen and Goring-Morris (2010) outline three distinct zones of PPNA, the south-central Levant (and Damascus basin), the northern Levant (Orontes valley and middle Euphrates) and an upper Tigris/Zagros zone (cf. ‘core area’), with differences of material cultural from the start of the PPNA. The southern zone may have had more of an early emphasis on emmer wheat, with barley, lentils and various local lost crops, while the northern Levant cultivators were more prone to focus on two-grained einkorn, and rye, as well as barley and peas. The ‘core area’ seems to have taken to all of these, but apparently from local wild sources. While these regions become increasingly interlinked as a ‘PPNB Koine’ (Goring-Morris and Belfer-Cohen 2010; see also Asouti 2006), there remained distinct regional cultural traditions, which are not easily derived from the spread of farmers from a single restricted core. The so-called ‘core’ region, which sits at the crossroads of the eastern fertile crescent, the western fertile crescent, the upper Mesopotamian river valleys and eastern Anatolia, would appear to have been in prime position for bringing together a diverse range of crop varieties and early livestock from surrounding regions, as well as drawing on its broader range of wild progenitors. This may make it an important area of later integration of food production, but this does not make it the centre of origin.

Multi-focal agricultural origins: a worldwide pattern

Thus the package of founder crops (and some lost crops) was not found growing wild and brought into cultivation as one prescient invention, but instead was assembled piecemeal and gradually over an extended period of millennia together with livestock and latecomers such as olive and almond. Other parts of the world suggest similarly multi-focal processes, with many instances in which only a single crop was initially cultivated, undermining the inference of Abbo et al. (2010, 2011) that an overlapping package of crops was a necessary condition of early agriculture, and that therefore the region of overlap of wild progenitors should outline a domestication ‘core’.

Whether we accept only nine or ten centres (e.g. Diamond 2002) or accept that there could have been as many as twenty or twenty-four (Purugganan and Fuller 2009), it seems clear that agriculture was not invented once and only once. When looked at in detail each of these ‘centres’, like the Near East, begins to look like a regional mosaic, or a ‘non-centre’ in Harlan’s (1971) terms. A full review of these origins is beyond the scope of the present comments, but it is worth noting that in many instances multiple domestications are indicated for the better-documented species, and that large complementary packages of crops are not a prerequisite for cultivation. Take the case of rice, where it is clear that *japonica* and *indica* had distinct genetic (e.g. He et al. 2011), ecological and geographical backgrounds, and plausibly *japonica* was brought into cultivation in more than one region of China prior to evidence for cultural contacts (Fuller et al. 2010a). It is also clear that rice was cultivated alone, supplemented only by wild plants like acorns and fruits (Fuller and Qin 2010). Rice became a major staple dispersed through China and Southeast Asia, but mainly as a solitary domesticate and not as part of a complementary crop package, since soy beans, azuki beans or other proteinaceous crops appear to be much later

additions from other regions (cf. Crawford 2006). Chinese millets emerged as early or earlier than rice, appearing at or just after 6000 BC at widely dispersed north Chinese sites from Dadiwan in Gansu to Xinglonggou in Chifeng area of eastern Inner Mongolia: this evidence indicates not just independence from rice domestication but probably multiple distinct centres of early Chinese millet cultivation (Bettinger et al. 2010; Liu et al. 2009). India too has an archaeological record that suggests between three and five distinct regional focuses of early cultivation (Fuller 2006), including Gangetic rice management and differing local packages of millets and pulses in the savannah zones.

Africa provided Harlan (1971) with his classic example of an agricultural non-centre, since his own study of wild progenitors indicated that they had widely non-overlapping distributions in the savannahs, forest margins and sahel (see Marshall and Hildebrand 2002). In another case like that of rice, West African pearl millet (*Pennisetum glaucum*) was cultivated alone, without complementary crops (Kahlheber and Neumann 2007). It had two focuses of early cultivation and possible domestication, one in the Sahel of northeast Mali in the third millennium BC (Manning et al. 2011) and the other in southeast Mauretania, which appears culturally unconnected (MacDonald et al. 2009). These two potential pathways into pearl millet cultivation are clearly distinct from the eastern savannah region (between Lake Chad and Ethiopia) which is postulated for sorghum domestication. The arrival of both sorghum and pearl millet in India before 1700 BC (Fuller and Boivin 2009) implies broadly similar mid-Holocene domestications across sub-Saharan Africa, while additional native millet domestications (tef, finger millet) in the Ethiopian uplands remain poorly documented (e.g. D'Andrea 2008; Giblin and Fuller 2011).

Farther afield new evidence coming from Amazonian crops is showing a parallel and similarly complex situation (e.g. Clement et al. 2010) even if modes of domestication, reproduction and cultivation are very different. Archaeobotanical and archaeological data are scarce in the area (but see Dickau 2009; Pickersgill 2007; Piperno 2009), but the contrast between the presumed areas of origin of native Amazonian crops in peripheral zones and the areas of high genetic diversity at the time of European conquest suggest a long and complex history of early cultivation and later intensified production (Clement et al. 2010). Evidence for the appearance of a number of Amazonian domesticates, including peanuts, on the dry Peruvian coast by c. 7000 BC (Dillehay et al. 2007), implies that these were brought into cultivation in the Amazon earlier still and well before the arrival of maize and other crops from central American domestication pathways.

A shared Pleistocene cultural inheritance provides proclivities for agriculture

We hypothesize that the reason domestication happened in parallel numerous times is that human groups drew upon a collective memory and deep cultural traditions of plant tending, when ecological and social circumstances warranted. There is no reason to doubt that all hunter-gatherers understood how plants reproduce and multiply, whether it be by seeds or by tubers. Ethnographic evidence strongly indicates this even in regions that never had prehistoric traditions of agriculture, such as Australia (e.g. Harris 1977, 1989; Steensberg 1986). We would posit that helping plants multiply and manipulating landscape compositions was part of the collective memory of *Homo sapiens sensu stricto*

since the Middle/Upper Palaeolithic, and that such knowledge has been passed down to recent hunter/gatherers who practised such techniques in different parts of the world. However, in the absence of sedentism and large-scale systematic processing of particular species (like cereals), little is preserved of such activities in the archaeological record. Nevertheless there are two lines of circumstantial evidence that point to this, including Pleistocene evidence that *Homo sapiens* tended to manage landscapes by burning vegetation and had presumably cultivated and certainly trans-located the bottle gourd from its wild range in Africa sometime in the Pleistocene.

While use of fire on a local scale, e.g. for cooking, is associated with *Homo erectus* on the order of at least 700,000 years ago (Alperson-Afil 2008; Wrangham 2009), anatomically modern humans used fire systematically to alter vegetation (Mellars 1976; Pyne 2001; Rowley-Conwy and Layton 2011). This is reflected in massive upturns in sedimentary micro-charcoal record. In island Southeast Asia and Australia for example, this upturn in burning takes place between 60,000 and 50,000 years ago, with the arrival of modern humans (Thevonon et al. 2004). A similar massive increase is seen in micro-charcoal records in the Americas (e.g. Panama) starting just before 13,000 cal. BP and therefore correlated with human arrival or significant inland colonization of the Americas from early coastal/lowland populations (Piperno et al. 1990).

The bottle gourd is now derived from a wild African species and genus (Decker-Walters et al. 2004), but had reached America before the start of the Holocene. Ancient DNA evidence derives all prehistoric American bottle gourds from those of East Asia (Erikson et al. 2005), while archaeological finds in early Holocene America and East Asia both point to this species having been selected for thicker rinds than its wild African ancestor prior to the development of other domesticated plants (Fuller et al. 2010c). This indicates that Pleistocene humans moved gourds from their African homeland to Asia and later America, and cultivated them with selection for thicker rinds. There were presumably other tended and translocated plants which we are so far unable to detect, but the key point is that there is no reason to believe that sowing and tending of plants was a great idea of a few core area foragers of the early Holocene upper Tigris valley, but instead it was shared ancestral knowledge of *Homo sapiens* which could be drawn upon as local circumstances warranted. In settings in which this became routine and systematic, it set in train increasing dependency on the part of human populations and selection for morphological adaptation on the part of plants resulted.

Conclusions

Modern human hunter-gatherers were well versed in landscape management and understood the life histories of plants. Hunter-gatherers are compulsive niche constructors, modifying environments for their own benefit and passing both that modified environment and the cultural practices of management onto subsequent generations (e.g. Rowley-Conwy and Layton 2011; Smith 2007, 2011; Wollstonecroft 2011). Technological developments, such as grinding or vessels for boiling, made some food more nutritionally valued and hence accessible (Fuller and Rowlands 2009; Rowlands and Fuller 2009; Wollstonecroft 2011; Wollstonecroft et al. 2008). Thus technological developments in food

processing may have been an important part of the cumulative cultural trajectory in niche construction over the later Pleistocene which laid the groundwork for the strategic shifts to cultivation of food crops. With increasing social complexity, population densities and subsistence diversity, numerous regional populations started strategies of resource management and 'low-level food production' (*sensu* Smith 2001; also Rowley-Conwy and Layton 2011). In many cases this did not lead on to domestication and agricultural dependence, but in some contexts the feedbacks between labour committed to cultivation, genetic adaptations of the plant (morphological domestication) and increased food acquisition pulled populations that started down this path increasingly into reliance on cultivation, i.e. the cultivation's labour 'traps' (Fuller et al. 2010b). The role of external environmental stresses in any given case requires investigation. In the Near East, proponents of a Younger Dryas environmental push have been many (e.g. Bar-Yosef 2003; Haldersen et al. 2011; Hillman et al. 2001; Rowley-Conwy and Layton 2011), although the generally delayed evidence for cultivation and even later plant domesticates (see above) calls this single prime mover into question. Increasingly Abu Hureyra appears to be the exception, rather than the rule, and presents an ambiguous case for a Younger Dryas era shift to cultivation (Colledge and Conolly 2010; Willcox et al. 2009). But PPNA cultivation was widespread and an early stage on a slow millennial road to domestication and agriculture. This slower trajectory of domestication may well imply varied pressures for and against agriculture along the way.

The evidence from the Near East indicates that the mosaic of crop origins in the Near East was complex, as was that of animal domestication. There is still much work to do: we have only the fragmentary beginnings of a picture of agricultural origins even in this best studied region. The picture here suggests that there is even more exciting research ahead on agriculture.

Dorian Q Fuller

Institute of Archaeology, University College London
d.fuller@ucl.ac.uk

George Willcox

CNRS

Robin G. Allaby

University of Warwick

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Dorian Q Fuller, FLS FSA, is Reader in Archaeobotany at the Institute of Archaeology, University College London. He completed his PhD at Cambridge on the origins of agriculture in South India, and has subsequently worked on archaeobotanical material and plant domestication studies in India, China, Sudan, West Africa and the Near East. He is co-author of the book *Trees and Woodlands of South India: Archaeological Perspectives* (Left Coast Press, 2008) and edits the journal *Archaeological and Anthropological Sciences*.

George Willcox is a senior researcher with the Centre National de la Recherche Scientifique of France. He has been working on Near Eastern archaeobotany for nearly forty years, and has conducted archaeobotanical research on thirty-five sites in the region. He co-edited the volume *The Origins of Agriculture and Crop Domestication* (ICARDA, Aleppo, 1999). He is on the editorial board of the journal *Vegetation History and Archaeobotany*.

Robin G. Allaby, FLS, is an associate professor at the University of Warwick. He completed his PhD on ancient DNA and phylogenetics of wheat at the University of Manchester. His research focuses on the evolution and adaptation of crops using genetics, ancient DNA and modelling systems. He is on the editorial board of *Archaeological and Anthropological Sciences*.