



Revisiting the concept of the ‘Neolithic Founder Crops’ in southwest Asia

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Abstract

Zohary and Hopf coined the term ‘founder crops’ to refer to a specific group of eight plants, namely three cereals (einkorn, emmer and barley), four legumes (lentil, pea, bitter vetch and chickpea), and a fibre/oil crop (flax), that founded early Neolithic agriculture in southwest Asia. Zohary considered these taxa as the first cultivated and domesticated species, as well as those that agricultural communities exploited and eventually spread to Europe and other regions. As a result, these eight species soon become the hallmark of the Neolithic plant-based subsistence. However, the ‘founder crops’ concept was defined at the end of the 1980s, when the development of agriculture was considered a rapid event, and therefore, terms like domestication, agriculture and plant cultivation were used interchangeably in the literature. The aim of this paper is thus to revisit concept of the ‘Neolithic founder crops’. Through a critical review of the archaeobotanical evidence gathered in the last 40 years, we evaluate the relative contribution of the ‘eight founder crop’ species to the plant-based subsistence across different periods of the southwest Asian Neolithic. We conclude that multiple groups of ‘founder’ species could be defined depending on whether one seeks to represent the most exploited plants of the Neolithic period, the first cultivated and domesticated crops, or the species that agricultural communities cultivated and eventually spread to Europe. Improved understanding of Neolithic plant-based subsistence in general, and agriculture in particular, will be attained by moving beyond conventional narratives and exploring the evolutionary history of plants other than the original ‘founder’ species.

Keywords Founder crops · Neolithic · Southwest Asia · Plant domestication · Lost crops · Agriculture

Introduction

The ‘founder crops’ concept was introduced by Zohary and Hopf in their pioneering book, *Domestication of Plants in the Old World*, to designate the plants that founded early Neolithic agriculture during the Pre-Pottery Neolithic B

period in southwest Asia (Zohary and Hopf 1988, pp. 1–2, Table 1). In the conclusion section of this book they write:

“The crops of early Neolithic agriculture in southwest Asia are fairly well recognised. The most numerous vegetable remains in early farming villages come from three cereals: emmer wheat (*Triticum turgidum* subsp. *dicoccum*), einkorn wheat (*T. monococcum* subsp. *monococcum*), and barley (*Hordeum vulgare*) [...] Several grain legumes appear as constant companions of the cereals. The most frequent pulses in the early Neolithic southwest Asian context are lentil (*Lens culinaris*) and pea (*Pisum sativum*). Two more local legume crops are bitter vetch (*Vicia ervilia*) and chickpea (*Cicer arietinum*) [...] Probably all four legumes were cultivated somewhat earlier, either together with wheats and barley or soon after the domestication of those cereals. Finally, flax (*Linum usitatissimum*) belongs to the Near East group of founder crops” (Zohary and Hopf 1988, pp. 207–208 as well as Zohary et al. 2012, pp. 1–2).

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Table 1 The eight founder crops and their wild progenitors as originally indicated by Zohary and Hopf (1988, see also Zohary et al. 2012)

Common name	Domesticated crop	Wild progenitor
Einkorn wheat	<i>Triticum monococcum</i> ssp. <i>monococcum</i>	<i>T. monococcum</i> ssp. <i>boeoticum</i>
Emmer wheat	<i>Triticum turgidum</i> ssp. <i>dicoccum</i>	<i>T. turgidum</i> ssp. <i>dicoccoides</i>
Barley	<i>Hordeum vulgare</i> ssp. <i>distichum</i>	<i>H. vulgare</i> ssp. <i>spontaneum</i>
Lentil	<i>Lens culinaris</i>	<i>Lens orientalis</i>
Pea	<i>Pisum sativum</i>	<i>Pisum humile</i>
Chickpea	<i>Cicer arietinum</i>	<i>Cicer reticulatum</i>
Bitter vetch	<i>Vicia ervilia</i>	<i>Vicia ervilia</i>
Flax	<i>Linum usitatissimum</i>	<i>Linum bienne</i>

Shortly after, in another publication, Zohary (1989) linked these eight species (Table 1) with the earliest cultivars, domesticated crops, as well as the first plants that were translocated and initiated agriculture in other regions. He wrote:

“(a) Three cereal crops: emmer wheat *Triticum turgidum* subsp. *dicoccum*, barley *Hordeum vulgare*, and einkorn wheat *Triticum monococcum* (in this order of importance) were the principal founder crops of Neolithic agriculture in this part of the world. Definite signs of their cultivation first appear in Southwest Asia (the Near East) in the 8th and 7th millennia BC.

(b) The domestication of these cereals went hand in hand with the introduction into cultivation of five companion plants: pea *Pisum sativum*, lentil *Lens culinaris*, chickpea *Cicer arietinum*, bitter vetch *Vicia ervilia* and flax *Linum usitatissimum*, all of which were very probably domesticated simultaneously with wheat and barley, or taken into cultivation just a short time later.

(c) The subsequent expansion of Neolithic agriculture to Europe, Central Asia and the Nile Valley was based on this same crop assemblage. The same crops that started food production in the Near Eastern ‘nuclear area’ also initiated agriculture in these vast territories” (Zohary 1989, p. 358; see also Zohary 1996).

In the 1990s and early 2000s the concept of the Neolithic founder crops was used to explain the origins of agriculture in southwest Asia and to justify the ‘core-area hypothesis’ for plant domestication (Lev-Yadun et al. 2000; Gopher et al. 2001; Abbo et al. 2010, 2012). According to this view, the eight Neolithic founder crops were selected and domesticated once, in a rapid event that took place in a single region or ‘core area’ located in southeast Turkey, as suggested primarily by some genetic studies (e.g. Ladizinsky and Adler 1976; Heun et al. 1997; Mori et al. 2003; Özkan et al. 2005; Luo et al. 2007). From here, domesticated or semi-domesticated plants (and consequently agriculture) radiated to other regions (Abbo et al. 2006; Kilian et al. 2007; Özkan et al. 2011). As such, these eight species were soon equated with the earliest (wild) cultivars (i.e. the species that “initiated

food production” in southwest Asia as indicated by Zohary 1989, 1996), the species that were first domesticated, as well as the crops that fully-fledged Neolithic agricultural economies exploited and eventually spread to other regions (see Table 2, and also Lev-Yadun et al. 2000; Gopher et al. 2001; Abbo et al. 2005; Abbo and Gopher 2020).

However, archaeobotanical advances in the last decades have made clear that to fully understand the origins and development of food production in southwest Asia, it is necessary to separate biological processes like plant domestication from management practices like plant cultivation and socio-economic systems like agriculture (see Harris 1996; Fuller 2007; Harris and Fuller 2014; Fuller et al. 2018). Plant domestication makes reference to a biological phenomenon, represented by a series of phenotypic changes that result from the adaptation of the plants to human-made habitats (Fuller 2007; Harris and Fuller 2014; Fuller et al. 2018). In accordance with previous definitions, domestication and cultivation are related as cause and effect (Harris and Fuller 2014, p. 105). In our view, plant cultivation (i.e. sowing) would represent one of the many plant management practices that could have taken place in the past, and it would essentially make reference to an economic activity (see Table 3). Agriculture instead represents the end result of the combination of plant cultivation and domestication (Harris and Fuller 2014; Fuller et al. 2018). It makes reference to a new subsistence strategy or way of life (Table 3), and it was the ultimate consequence of a long-term or protracted process that initiated (necessarily) with the management of morphologically wild species (i.e. pre-domestication cultivation), and which brought significant transformations in human economy and society, as well as impacts in the surrounding environment (see Harris 1996; Harris and Fuller 2014; Fuller et al. 2018). Overall, the fact that the ‘founder crops’ concept was defined at the end of the 1980s, when the ‘core-area/ short gestation’ model for the development of agriculture was the main explanatory model and terms such as plant cultivation, domestication and agriculture were used interchangeably in the literature, means that we have to revisit its meaning in the light of the key scientific advances made in the last decades.

Table 2 Different terms and processes used to define the ‘founder crops’, and the associated chrono-cultural periods based on the archaeobotanical evidence we have nowadays

Association between the 'founder crops' and the...	Reference	Chrono-cultural period assigned based on the evidence gathered to date
Crops of early Neolithic agriculture	Zohary and Hopf 1988 (p. 207), see also Zohary et al. 2012	The early Neolithic agriculture makes reference to the MPPNB-PPNC (10.2-8.5 ka cal BP). Zohary and Hopf seemed to exclude the Late Neolithic (Pottery Neolithic) agricultural period (8.5-6.5 ka cal BP) from the 'founder crops' concept
Most numerous remains in early farming villages	Zohary and Hopf 1988 (p. 207) see also Zohary et al. 2012	It is now known that early farming villages develop c. PPNA/EPPNB (11.6-10.2 ka cal BP)
Species that initiated food production in southwest Asia	Zohary 1989 (p. 358)	It is now known that early food production (e.g. cultivation) started during the PPNA (11.6-10.7 ka cal BP)
Most frequent... in the Early Neolithic southwest Asian contexts	Zohary et al. 2012 (p. 1)	The Early Neolithic makes reference to the PPN period, including the PPNA and the PPNB/C (11.6-8.5 ka cal BP)
First definite sign of plant cultivation	Zohary and Hopf 1988, (p. 207)	Plant cultivation seems to have been first practiced during the PPNA (11.6-10.7 ka cal. BP)
The initiation of food production... is based on the domestication of a relatively small number (8-9) of local grain plants	Zohary and Hopf 1988 (p. 207), see also Zohary 1989, 1996	We now know that food production initiated in the PPNA, but first domesticates (i.e. non-shattering cereals) appear primarily during the EPPNB (10.7-10.2 ka cal BP), that is, before the development of agriculture
Common package of grain crops characterizes the development of agriculture	Zohary et al. 2012 (p. 2)	It is inferred that agriculture developed c. 10 ka cal BP (during the MPPNB)
Crops that spread with agriculture	Zohary and Hopf 1988 (p. 209), see also Zohary 1989, 1996; Zohary et al. 2012	This could make reference to the PPNB, but the evidence found in Cyprus indicates that crops started to spread before the development of agriculture, at least c. 10.8-10.6 ka cal BP (Vigne et al. 2012)
Founder crops that started agriculture... during the Pre-Pottery Neolithic (PPN) period, some 11,000-10,000 years ago	Weiss and Zohary 2011 (p. S237)	The chronology indicated by the authors makes reference to the periods before agriculture, comprising the PPNA and the EPPNB, as well as the first two centuries of the MPPNB

PPN Pre-Pottery Neolithic, *PPNA* Pre-Pottery Neolithic A, *EPPNB* Early Pre-Pottery Neolithic, *MPPNB* Middle Pre-Pottery Neolithic, *PPNC* Pre-Pottery Neolithic C

Thus, the general aim of this paper is to reevaluate the meaning of the ‘founder crops’ concept. In particular, we seek an answer for a number of key questions like: What does this concept exactly refer to? Do these eight crops represent the ‘most numerous vegetable remains at early farming sites’ as originally claimed by Zohary and Hopf? Were they the first cultivated and domesticated plants? Does this crop package represent the plant species that founded Neolithic agriculture in southwest Asia and they were eventually translocated to other regions? To answer these question we consider the archaeobotanical evidence published in the last forty years, and assess the role that these species played at Neolithic sites dated to between 11.6 and 6.5 ka cal BP. We examine the quantitative data for species occurrence for different plant categories (grasses, legumes, fruits and nuts, and other wild plants) and evaluate the species that were primarily exploited during the different phases of Neolithic period. We also consider the qualitative archaeobotanical data for plant cultivation and domestication, and define the group of species

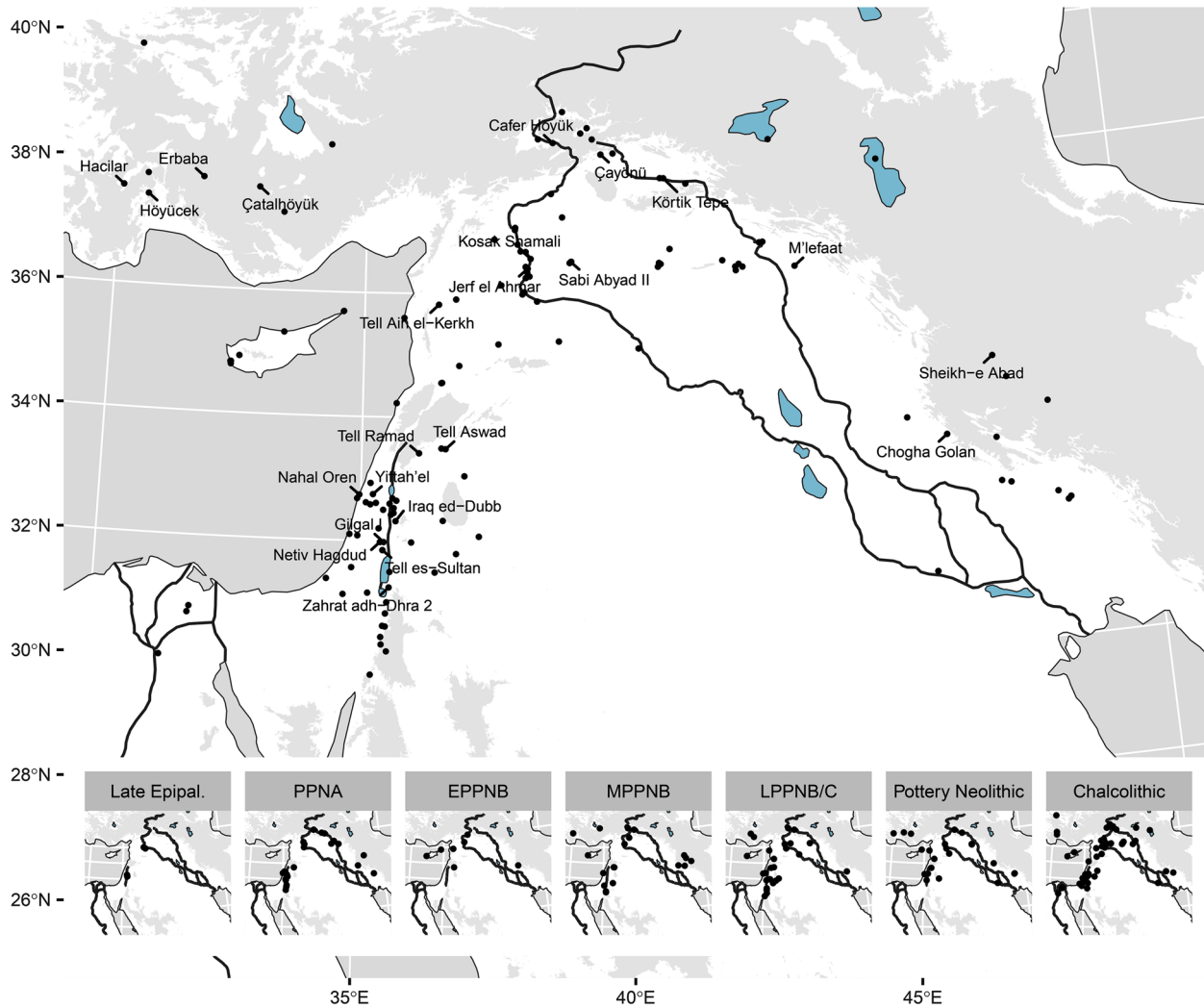
that, based on the information available to date, seem to have been first cultivated and domesticated in southwest Asia, as well as those that Neolithic agricultural communities exploited and spread to other regions. We conclude the paper by drawing some final reflections on the founder crops concept, highlighting the research biases related to the overall characterization of the Neolithic plant-based subsistence, and suggesting a number of new avenues for future research.

Materials and methods

In this paper we evaluate four main processes: plant exploitation practices (i.e. including economic uses as food, fodder, raw materials etc.); management of plant resources (which can involve activities like cultivation, pruning, coppicing etc.); biological evidence for plant domestication (i.e. morphological changes that separate

Table 3 Classification of the terminology used in this work (to be read in columns)

Chrono-Cultural periods	Subsistence strategies	Economic activities	Biological form
Epipalaeolithic	Foraging	Plant gathering	Wild
Neolithic	Agriculture	Plant management: <i>cultivation (i.e. sowing), coppicing, pruning, irrigation, manuring, tilling...</i>	Domestic
Chalcolithic	Horticulture		...
Bronze Age	Pastoralism	Plant use: <i>food, fuel, raw materials...</i>	
...	

**Fig. 1** Distribution of sites included in the meta-analysis

wild, semi-domestic and domestic species); and the translocation or spread of crops and other plant resources to non-native regions. To identify and characterise each of these aspects both qualitative and quantitative data is considered.

Plant exploitation practices

To test whether Zohary and Hopf's statement holds true, i.e. that the founder crops were the "most numerous vegetal remains" at early Neolithic/agricultural sites in southwest Asia (1988, p 207) we primarily examined plant species ubiquity and frequencies (see section 'Were the founder crops the "most numerous" plants?' below). Our quantitative

Table 4 Number of sites and assemblages included in the meta-analysis by period

Period	Ka cal BP	Subsistence	N sites	N assemblages
Late Epipal	15–11.7	Foraging	4	6
PPNA	11.7–10.7	Pre-domestication cultivation	23	27
EPPNB	10.7–10.2	Cultivation of domesticated species	8	9
MPPNB	10.2–9.5	Cultivation of domesticated species	20	34
LPPNB/C	9.5–8.5	Agriculture	29	40
Pottery Neolithic	8.5–6.5	Agriculture	23	33
Chalcolithic	6.5–5	Agriculture	58	86

Neolithic periods in bold

analyses are based on a comprehensive dataset of previously published species occurrence data from the Neolithic of southwest Asia. A compendium of R code and data supporting this meta-analysis is available at <https://doi.org/10.5281/zenodo.5911218> and described in ESM 1. The processed data underlying the analyses are also included in ESM 3.

We collated raw data from three existing regional databases: the *Archaeobotanical Database of Eastern Mediterranean and Near Eastern Sites* (ADEMNES, Riehl and Kümmel 2005); the database of the *Comparative Pathways to Agriculture* project (COMPAG; Lucas and Fuller 2018; Fuller et al. 2018), which incorporates an earlier dataset compiled by Colledge, Connolly, and Shennan (Colledge et al. 2004; Shennan and Connolly 2007); and the *Origins of Agriculture* database (ORIGINS, Wallace et al. 2018). All assemblages from sites in Southwest Asia and dated to the Neolithic period (11.7–6.5 ka cal BP) according to the source databases were integrated. Site names were standardised across databases to prevent duplication of the same assemblages, and where the same site was found in multiple databases, we included only the most recent and detailed records (i.e. ORIGINS was preferred over COMPAG over ADEMNES). In total, our meta-analysis includes 135 sites, 78 of which have Neolithic phases, distributed fairly evenly across Southwest Asia (Fig. 1)—though the Southern Levant and Upper Euphrates are somewhat over-represented, especially in earlier periods.

Our collated dataset covers six key chrono-cultural periods: the Pre-Pottery Neolithic A (PPNA), early Pre-Pottery Neolithic B (EPPNB), the middle Pre-Pottery Neolithic B (MPPNB), the late Pre-Pottery Neolithic B (LPPNB), Pre-Pottery Neolithic C (PPNC), and the Pottery Neolithic (PN). It should be noted that in regions like Anatolia, southeast Turkey, Iran and Iraq, these chrono-cultural phases are not always recognised and terms like ‘Aceramic Neolithic’ are used instead. We also included assemblages from the preceding Late Epipalaeolithic period (15–11.7 ka cal BP) and succeeding Chalcolithic period (6.5–5 ka cal BP) in portions

of the analysis that might otherwise be distorted by the ‘edge effect’ of a strict cut-off date.

The chronological resolution of our analysis was determined by the level of detail available in the source databases, and since only the ORIGINS database included sample-level data, we selected aggregated assemblages from individual ‘site-phases’ as the common unit of analysis (e.g. Nahal Oren PPNA, Nahal Oren PPNB, ...), though many sites were recorded as having only one phase. The assemblages were assigned to both a cultural period (e.g. PPNA, PPNB etc. see Table 4) and to a calendar century based on the absolute chronological information available in the source database. 240 assemblages were included in total, including 145 from the Neolithic.

Taxonomic information was standardised across the source databases using a thesaurus of variant names—where possible to a specific species, and at least to genus, with one exception: potentially edible but otherwise indeterminate members of the Brassicaceae family were included, given the difficulties of identifying these taxa.

To this we added further classifications of each record by plant category (grasses, fruits and nuts, pulses, and ‘wild plants’), status as a founder crop or progenitor, edibility, and seed size (for grasses and legumes). Wood remains were excluded. The lack of sample-level data in two of the source databases limited the quantification strategies available to us, so all our analyses are based either on presence or relative proportion per site-phase assemblage. From these we derived two main measures of cross-assemblage ubiquity and abundance, respectively: the proportion of assemblages in which a taxon or group of taxa is present (or constitutes greater than a quarter of the assemblage, or a half, etc.); and the average proportion or relative frequency of a taxon or group of taxon across assemblages. We rely primarily on per-assemblage proportions because it is the only statistic that can be feasibly calculated for all assemblages, given the scale of our analysis. We acknowledge that in prioritising a large sample size and broad spatio-temporal coverage, our approach inevitably sacrifices precision and the possibility

to consider site-specific contextual factors. Still, we believe this is a trade-off worth making, given that this approach is relatively under-represented in the regional literature compared to ‘high precision, modest sample size’ studies, and that the conclusions we have drawn stand despite the limitations of the data and method (see also Colledge et al. 2005). In total, occurrence data on 457 taxa were included in the meta-analysis.

The interpretation of ubiquity and frequency data is not straightforward. In this work, ‘intense exploitation’ is inferred from high ubiquity and frequency values, but it is acknowledged that multiple factors including different plant uses, preservation, sampling strategies, recovery methods, quantification approaches etc. can affect these values (see Popper 1988). Previous studies show that, despite the complex taphonomic histories of archaeobotanical assemblages in southwest Asia, statistically significant patterns can be obtained when comparing multiple sites in a broad perspective (see Colledge et al. 2004, 2005; Fuller et al. 2018; Wallace et al. 2019). Nevertheless, in depth examination of how taphonomic factors affect archaeobotanical assemblages at a site level are necessary to understand the compositional variation of archaeobotanical assemblages (Colledge et al. 2004, p S46). Our previous review evaluating taphonomic factors at 27 Epipalaeolithic and Neolithic sites indicated that archaeobotanists reported recurrent patterns, with clear tendency towards the over-representation of Boraginaceae species (which have a siliceous outer coat that make them more resistant), *Ficus* spp. (which produces a large number of seeds, and these are often individually quantified, i.e. 1 item 1 score) and to a lesser extent *Pistacia* spp. (the wood of which has been intensively used as fuel, leading to concentrations of pistachio nut shells at some sites) (supplement text S1, supplement Table S2 in Arranz-Otaegui et al. 2018a). In addition, carbonate-rich endocarps of *Celtis* sp. can also tend to over-representation, as they naturally resist decay (see Fairbairn et al. 2014; Baird et al. 2018). As such, to limit both the over/under-representation of specific taxa, as well as the discrepancies between taxa targeted for the seeds *versus* those targeted for fleshy fruits, in this study we made comparisons primarily between species within the same plant category (i.e. cereals, pulses, wild plants etc.), and highlighted particular cases where taxa over-representation was made clear by the original archaeobotanist.

Plant management and domestication

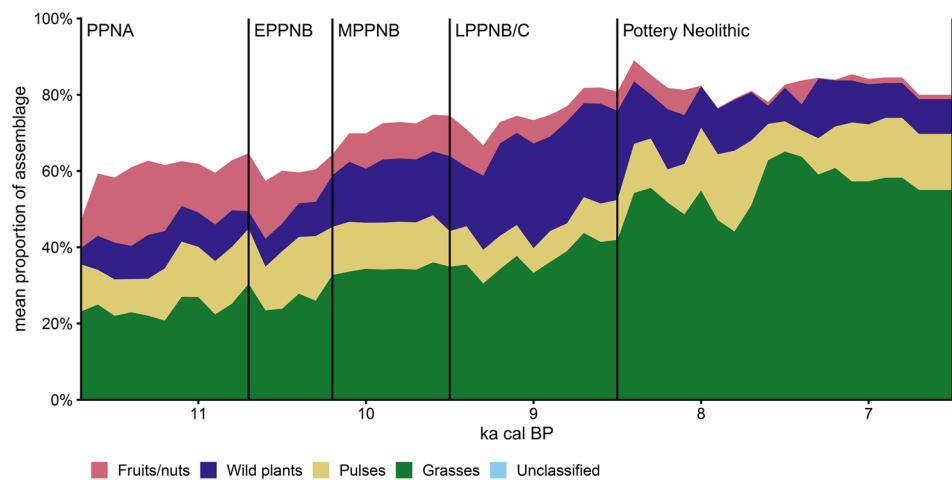
To evaluate whether the eight founder species were the earliest group of plants cultivated and domesticated, we also undertook a qualitative assessment of the evidence for plant management and domestication. We followed a species-by-species approach, separating the taxa for which evidence of management and domestication has been studied, from the

plant species that show ubiquity and frequencies similar or even higher than those reported for the founder crops, but for which detailed studies have not been yet carried out. The site-by-site data for each of the founder cereal/legume species has been previously gathered and summarised in Arranz-Otaegui (2015). This has now been updated, and it includes a total of 86 Epipalaeolithic and Neolithic site/phases (see ESM 2, Tables 1–9).

We define plant management as a set of activities that increase or improve the overall harvest yields. Plant management may involve practices like cultivation (i.e. sowing), tillage, pruning, coppicing, manuring and irrigation among others, but direct identification of these practises in the archaeological record is still limited. As such, in this study we evaluate the evidence for the cultivation of cereals and pulses, as well as discuss several studies reporting the possible management of other plant resources. The identification of pre-domestication cultivation in the archaeological record primarily involves cereals, and its identification relies on the presence of plump or cultivated/domestic-type grains (i.e. they are considered ‘pre-domestic’ as they have not still developed tough-rachises, which represents the key trait of domestication, see Hammer 1984; Hillman and Davies 1990; Fuller 2007). In addition, other secondary evidence such as the presence of potential arable flora, storage structures, reduction in ‘gathered’ plant resources, and large concentrations of plant remains has also been taken into account to infer early cultivation practices (see rationale in Colledge 2001; Willcox et al. 2008).

Domestication refers to a biological process driven by human action, and which produces a number of different phenotypic changes (*sensu* Hammer 1984; Hillman and Davies 1990; Fuller 2007; Harris and Fuller 2014). To identify domesticated cereals the proportion of non-shattering (i.e. domestic-type) rachis remains was evaluated. As in previous works, proportions of non-shattering < 10% were considered representative of wild populations, and above that threshold, primarily > 20%, as representative of populations in process of domestication (see also Kislev 1989a; Tanno and Willcox 2006a, b, 2012; as well as Fuller et al. 2018, who consider > 80% non-shattering along with > 20% increase in average crop seed size as representative of full domestication). The identification of domesticated legume species in the archaeological record is not straightforward. Key traits include pod indehiscence and smooth testa (Zohary and Hopf 1973; Butler 1995, 2009), but these are not commonly preserved or systematically recorded. In fact, Zohary et al. (2012, p. 2) acknowledge that “pulses usually lack morphological features by which initial stages of domestication can be recognized”. As such, indirect evidence, like the recurrent presence of legume species in storage contexts and the intense exploitation of particular species, is discussed. These practises would not have been possible in populations that

Fig. 2 Abundance of plant categories in Neolithic assemblages through time



did not previously developed key domestication traits like non-dormancy and indehiscence (the presence of large grain sizes in pulses is instead more difficult to evaluate and its interpretation varies depending on the species under study). Criteria and data to evaluate domestication processes in plant categories like ‘the wild plants’ and fruits and nuts during the Neolithic in southwest Asia is currently very limited, and often relies on the presence of plants outside their wild natural range (see Zohary et al. 2012). Nonetheless, the available data has also been integrated.

In this work, agriculture is defined as a socio-economic system that relies primarily on the cultivation of domesticated crops (as previously defined by Harris 1996; Harris and Fuller 2014). Agriculture is linked to several management practices such as tillage, manuring, irrigation etc. which go hand in hand with significant changes in demography (increased population), society (shifts in social organisation, work force and food storage), and human impacts in the landscape (due to grazing, land-cultivation and woodland exploitation). In southwest Asia, the development of agriculture is thought to have crystallised during the Middle Pre-Pottery Neolithic B, ca. 10.2–9.5 ka cal BP.

Species translocation

To evaluate whether the eight founder crops were the first plant species that spread or were taken into other regions, we considered the earliest records for plant species outside their natural distribution in southwest Asia (as recorded by Zohary et al. 2012). Some of the wild relatives (e.g. *Hordeum spontaneum*, *Pisum*, *Lens* etc.) have wide natural distribution areas, so for these we looked beyond Greece and Cyprus for evidence of translocation. Archaeological examples were extracted from an existing compilation of archaeobotanical data from Europe (Colledge et al. 2005), with absolute dates estimated from the relevant literature cited in that dataset.

Results

Were the founder crops the “most numerous” plants?

The exploitation of plants during the Neolithic involved several plant categories, including grasses, legumes, wild plants, and fruits and nuts. Results show large differences in terms of the frequencies of the different plant categories and species exploited over time (see detailed descriptions in ESM 1).

In terms of abundance and ubiquity values, grasses were the most common plant category present during the Neolithic (average proportion of ca. 41%), and in 34% of the sites grasses made up more than half of the total plant remains recovered (see Table 3.3 in ESM 1). The second most common plant categories were the wild plants, followed by legumes and fruit and nuts. However, it has been shown that cereals and pulses are over-represented in charred assemblages, whereas the range of edible wild plant taxa is commonly incomplete, with losses in taxa diversity of up to 65% (College and Conolly 2004). This is an important aspect to highlight when it comes to interpretation, since it means that even at Neolithic sites where cereals and pulses predominate, wild plant resources could have still played a major role in subsistence.

Significant differences were also observed by period (Fig. 2 and Table 3.4 in ESM 1). During the PPNA, grasses become the most important plant category representing 30% of the assemblages. This contrasts with the previous Epipalaeolithic period, when plants in the ‘wild plant’ category were most commonly exploited, and grasses represented only 9% of the finds. During the EPPNB, the increase in the exploitation of grasses becomes more acute with values reaching up to 41%. It is also during this time that legumes become the second most exploited plant category and there is a significant

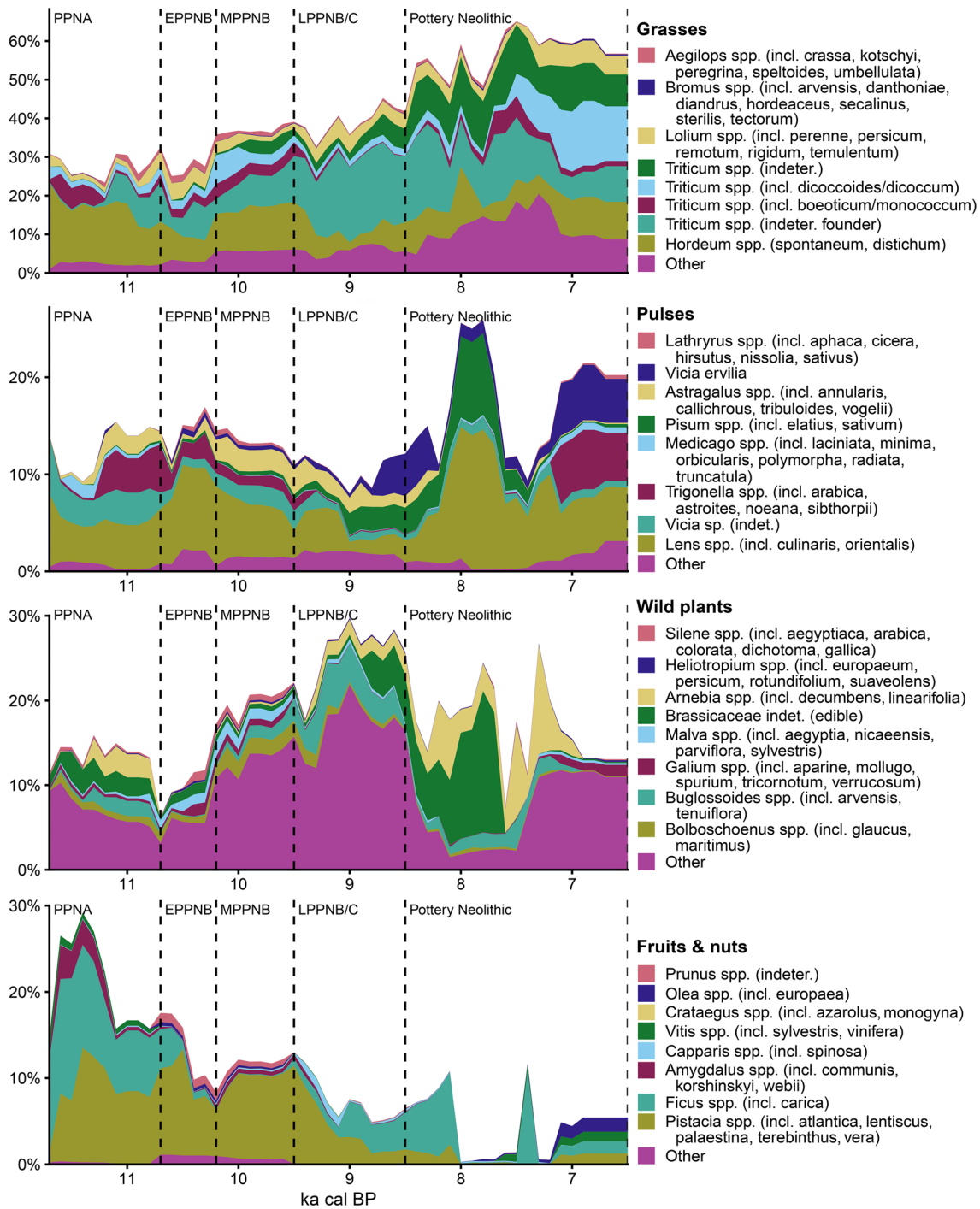


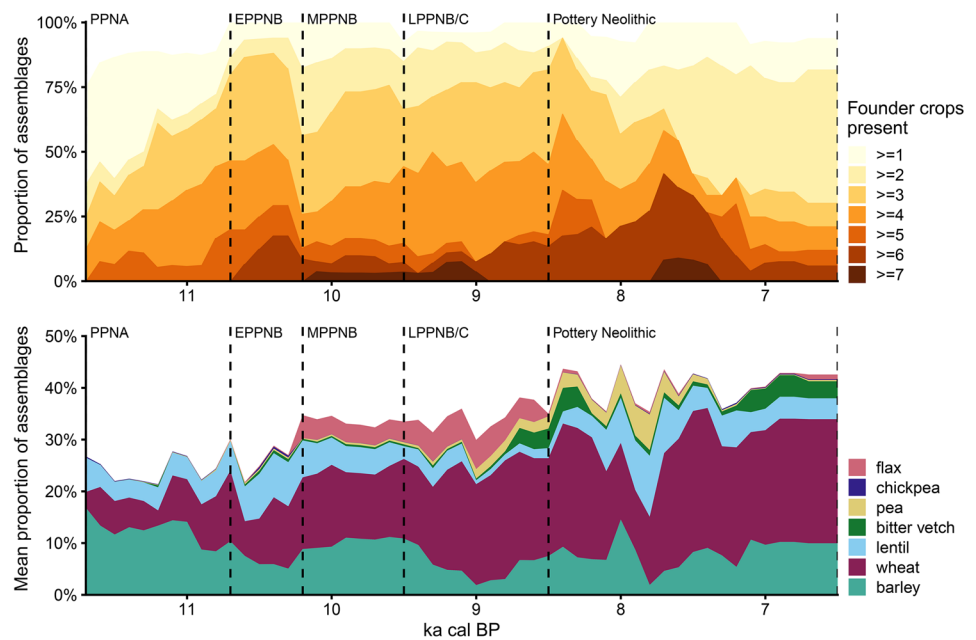
Fig. 3 Abundance (mean proportion of assemblage) of plant taxa by category in the Neolithic through time

decrease in the overall exploitation of wild plant resources (from 14% during the PPNA, to 7% during the EPPNB). The results also indicate that the exploitation of plants during the MPPNB, LPPNB/PPNC and Pottery Neolithic remained stable, with grasses gradually increasing their presence over time, and representing the most important plant category, followed by wild plant resources. Indeed,

it is not until the Chalcolithic period that the presence of wild plants decreased, and grasses and pulses became the two most recurrently exploited plant resources.

Grasses (Fig. 3, first panel)—the species that showed highest frequencies during the Neolithic are *H. spontaneum/distichum* and the founder *Triticum* spp. (i.e. einkorn and emmer). However, during the first millennia of the

Fig. 4 Cross-assembly ubiquity (top) and abundance (bottom) of founder crops in the Neolithic through time



Neolithic, the exploitation of *H. spontaneum* predominated, whilst from 10.5 ka cal BP the exploitation of *Triticum* spp. increased, and from ca. 10 ka cal BP this taxon became predominant. Within the wheat species, the exploitation of *T. dicoccoides/dicoccum* increased over time, with clear peaks around 10.5 ka cal BP and from 7.5 ka cal BP onwards, whereas *T. boeoticum/monococcum* was prevalent ca. 12–11.5 ka cal BP, but its presence fluctuated in subsequent phases. The presence of *Aegilops* spp., *Bromus* spp. and *Lolium* spp. remained stable during the whole Neolithic period, whilst other taxa including *Phalaris* spp., *Avena* spp., *Stipa* spp. and *T. aestivum/durum* (referred to as ‘Other’ in Fig. 3) gradually increased, especially from 8.5 ka cal BP onwards.

Pulses (Fig. 3, second panel)—*Lens* spp. was the most recurrently exploited taxon during the whole Neolithic period, with a clear peak around 8 ka cal BP. However, for the first 1,000 years of the Neolithic, i.e. until ca. 10.5 ka cal BP, non-founder taxa such as *Vicia* spp. and small-seeded legumes (primarily *Astragalus* spp. and *Trigonella* spp.) showed values similar to *Lens* spp. Moreover, until ca. 9 ka cal BP, several vetch species (e.g. *V. faba*, *V. narbonense*, *V. peregrina*) were more commonly exploited than founder species *Pisum* spp. and *Vicia ervilia*, whose exploitation increased only at the end of the Pre-Pottery Neolithic B/beginning of the Pottery Neolithic.

‘Wild plants’ (Fig. 3, third panel)—unsurprisingly, when it comes to wild plant resources, the most abundant taxa comprised species that are most resistant to post-depositional processes (e.g. Boraginaceae family including *Arnebia* spp., *Buglossoides* spp. and *Heliotropium* spp.). However, apart from these, the presence of *Bolboschoenus*

spp. is remarkable. This edible taxon seemed to have been intensively exploited from the beginning of the Neolithic until ca. 9.5 ka cal BP, when it started to decrease in terms of abundance. The Brassicaceae family was also recurrently exploited since the earliest phases of the Neolithic period. Its presence increased significantly from 9 ka cal BP onwards, with an important peak around 8 ka cal BP. It is also interesting to note that from 8.5 ka cal BP there is a marked reduction in the diversity of wild plant resources, and only the Boraginaceae family, the Brassicaceae family, and after 7.5 ka cal BP *Galium* spp. (a common weed of cultivated fields), maintained relatively high abundance values.

Fruits and nuts (Fig. 3, fourth panel)—*Pistacia* spp. and *Ficus* spp. were the most frequent taxa during the whole Neolithic period (but note that this might be in part the result of an over-representation of these two taxa, see Material and methods). However, chronological differences exist. From ca. 11.5 to 9 ka cal BP, *Amygdalus* spp., *Prunus* spp. and *Capparis* spp. seemed to have been exploited with some intensity, whereas after 9 ka cal BP, especially from 8 ka cal BP onwards, the exploitation of *Vitis* spp. and *Olea* spp. increased, and together with *Pistacia* spp. and *Ficus* spp., become the most commonly exploited taxa in the fruit/nut category.

In terms of ubiquity, of the 240 assemblages in our meta-analysis, only 3 (1.25%) report the presence of all of the founder crops, and none of these are dated to before the MPPNB. The cross-assembly ubiquity of the founder crops was generally low before this period, with peaks around the LPPNB-Pottery Neolithic, when around 25% of assemblages included 5 or more of the crops (see full data in Table 3.2 in ESM 1). If ubiquity statistics are evaluated on

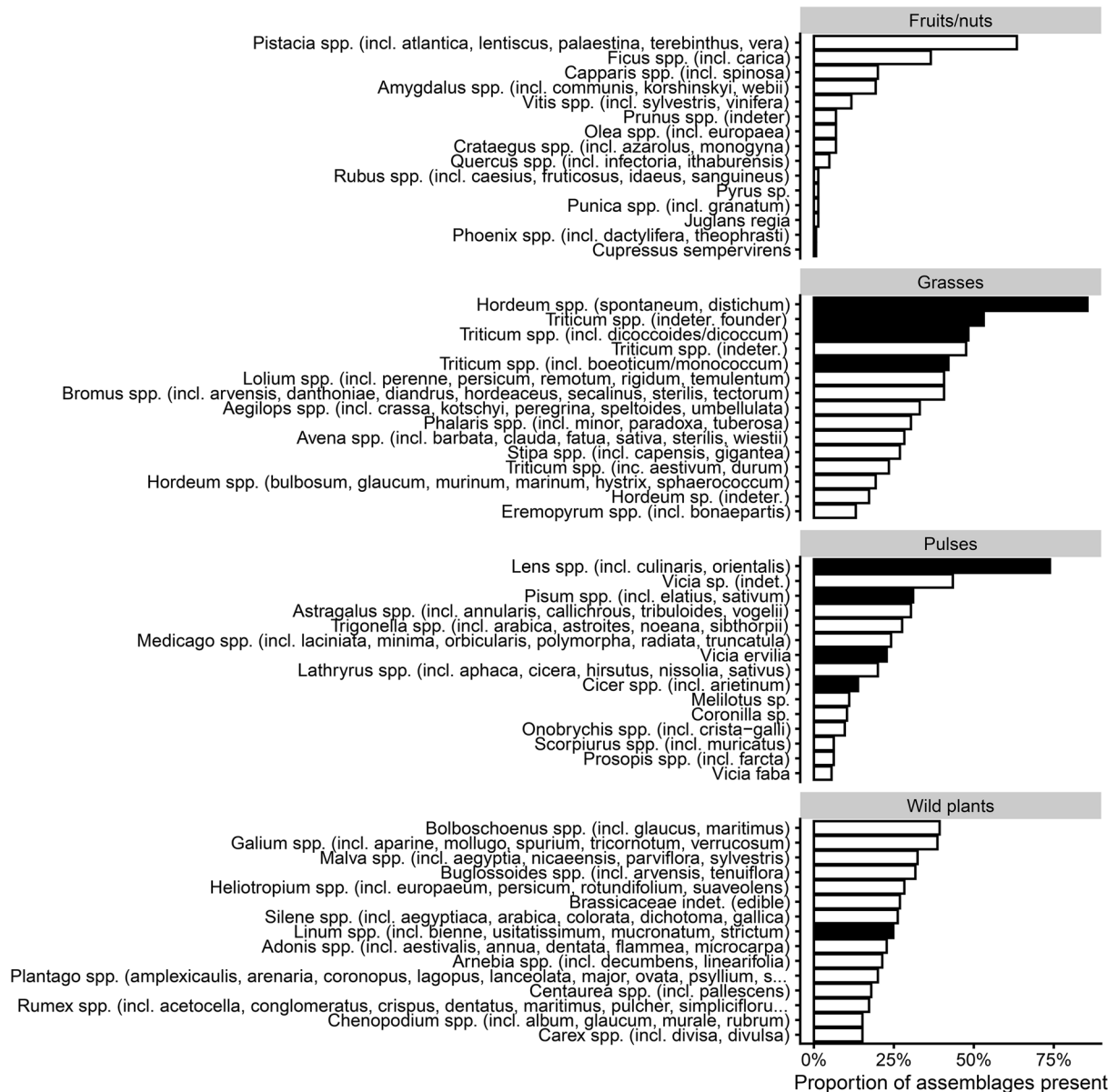


Fig. 5 Ubiquity of specific taxa across Neolithic assemblages. Founder crops in bold. Includes only the 15 most ubiquitous taxa in each category; for full data, see Table 3.1 in ESM 1

an absolute time scale (Fig. 4, upper panel), clear patterns emerged. As reported in our previous work (Arranz-Otaegui et al. 2018a), the exploitation of founder species was uncommon in the Epipalaeolithic and remained so during the first millennium of the Neolithic (the PPNA). It primarily developed during the EPPNB (ca. 10.5 ka cal BP), where there is an early peak in ubiquity, remaining relatively stable through the remainder of the PPNB, before another peak and subsequent decline in the Pottery Neolithic, ca. 7.5 ka cal BP.

The abundance (Fig. 4, lower panel) of different founder crop species also changed markedly over the course of the Neolithic (see Fig. 3.1 in ESM 1 for values by century).

The most dramatic trend was observed in *Triticum* spp., which went from comprising an average of less than 5% of assemblages at the beginning of the Neolithic, to nearly a quarter at its end. This is significant, as this shift alone could account for nearly all of the observed increase in founder crop abundance over the period. Abundance scores for *Hordeum spontaneum/distichum* fluctuated. Highest values were observed during the PPNA, the MPPNB, and the PN, whereas during the EPPNB and the LPPNB/PPNC a marked decrease was observed. *Linum* spp. began to appear ca. 10.2 ka cal BP but declined in use again ca. 8.5 ka cal BP. *Vicia ervilia* and *Pisum* spp. did not become abundant until

even later, during the second half of the Late PPNB/PPNC, ca. 9 ka cal BP. The case of *Cicer* spp. is paradoxical since the presence of this founder species is extremely rare during the whole Neolithic period.

If separated by species (Fig. 5), the most common founder crops, i.e. the taxa present in the largest number of sites, were *Lens* spp. and *H. spontaneum/distichum* present in ca. 68% of assemblages, closely followed by *T. dicoccoides/dicoccum* (44%), and *T. boeoticum/monococcum* (34%). The rest of the founder crops were comparatively less ubiquitous, with values similar to those reported for other edible plant species (see Table 3.1 in ESM 1 for the full data). *Vicia ervilia*, *Cicer* spp. and *Linum* spp. were the less ubiquitous founder taxa, present in between 22% and 12.5% of the Neolithic sites. Besides, the founder species were not even amongst the top 10 most ubiquitous plants exploited during the Neolithic. Edible taxa like *Pistacia* spp., *Ficus* spp., *Bromus* spp., *Lolium* spp., *Vicia* spp., *Bolboschoenus* spp. and *Malva* spp. among others, showed overall higher ubiquity values than several founder taxa. Besides, only in a very small number of cases (less than 5%) did any of the founder crop species make up more than a quarter of the archaeobotanical assemblages.

Were the founder crops the 'earliest' cultivated, domesticated and translocated species?

To evaluate the common belief that the founder crops represented the groups of plants that were first cultivated and domesticated in southwest Asia, as well as those that spread to other regions, in the following lines we review the archaeobotanical evidence for the management and translocation of plant resources during the Neolithic (see Tables 1–8 in ESM 2 for further information).

Grasses

There were at least eight cereal species taken into cultivation in the Neolithic, plus around five or six additional taxa that were recurrently exploited and could therefore have been managed.

Hordeum spontaneum/vulgare ssp. *distichum* (wild/domestic barley)

Wild barley was the most frequent cereal at PPNA sites in the Levant (see Table 1 in ESM 2), and it could have constituted a cultivar at sites such as Gilgal I (Weiss et al. 2006), where more than 260,000 grains were found in a storage context, and Jerf el Ahmar, based primarily on a gradual increase in grain size and the presence of arable flora (Willcox et al. 2008; although see Weide et al. 2022 for the interpretation of the arable flora at early Neolithic

sites). At one of the contemporary PPNA sites in the southern Levant, ZAD 2, relatively large numbers of domestic-type barley rachises were reported (ca. 30%), certainly larger than those that could be found in wild barley populations (Kislev 1989a), although the dataset comprises a relatively small number of chaff remains (Edwards et al. 2004). Thus, the clearest evidence for the presence of domesticated-type barley so far is recorded ca. 10.5 ka cal BP at EPPNB sites in central/southern Syria, with percentages of domestic-type barley rachises reaching up to 30–40% (Tanno and Willcox 2012; Arranz-Otaegui et al. 2016a). It is in these chronologies, ca. 10.8–10.6 ka cal BP, that barley is for the first time attested in Cyprus, and although this species could have been growing locally, it is suggested that it could have been introduced from mainland Levant together with emmer, and thus locally cultivated (Vigne et al. 2012). Barley is later reported outside the Fertile Crescent in a number of early Neolithic sites, such as Franchthi Cave in Greece (Asouti et al. 2018; see also Zohary et al. 2012).

Avena sterilis/sativa (wild/domestic oat)

Remains of wild oat have been found at a number of sites starting from the Epipalaeolithic period (Snir et al. 2015; Arranz-Otaegui et al. 2018a, b), but its contribution to subsistence is thought to have been minor except for the PPNA site of Gilgal I (Israel). Here more than 120,000 *Avena sterilis* grains were found in situ in a storage structure dated to ca. 11.5–11.1 ka cal BP, indicating their possible cultivation (Weiss et al. 2006). There is no doubt that this species played a major economic role at the site, but additional evidence, like metrical analysis of the grains, would help elucidate the status of oat as an early cultivar. Around 10.5–10.1 ka cal BP oat was translocated along with other cereals to Cyprus (Murray 2003), but the overall presence of this taxon during the Neolithic is rare, and its domestication is thought to have occurred during the Bronze and/or Iron Ages in Europe (Zohary et al. 2012).

Secale spp./*T. boeoticum thaoudar/urartu* (rye/wild two-grained einkorn and *T. urartu*)

Willcox (2004) showed that the size of *Triticum/Secale* grains, which mostly represented wild rye (see Willcox and Stordeur 2012; Douché and Willcox 2023), from PPNA Jerf el Ahmar increased from early to the later phases and was comparable to the domestic-type grain sizes documented at the Chalcolithic site of Kosak Shamali. This evidence along with a number of secondary data such as the presence of an arable flora and the location of the site beyond the natural habitats of wild rye, led the authors to conclude that it must have been subject to cultivation during the PPNA (Willcox et al. 2008). A recent publication using weed

functional analyses to discriminate between arable fields and wild cereal habitats indicates that the previously identified ‘weeds’ represented non-arable grassland communities, and that management practices, if ever carried out, would have entailed active re-sowing of cereals and their protection from grazers, but certainly not tillage (Weide et al. 2022). Nevertheless, wild rye was regularly exploited at contemporary sites in the Euphrates and northern Syria (Willcox et al. 2008; Willcox 2008), as well as later EPPNB (Douché and Willcox 2018, 2023) and MPPNB sites in the area (Hillman 1978; although see Fairbairn 2019 who reports the finds from Can Hassan as intrusive). Besides, the species is later attested in a number of Neolithic sites in Europe, including Cyprus ca. 6 ka cal BP (Kyllo 1982), although its presence increased primarily from the Bronze Age onwards (Gyulai 2014).

T. boeoticum/monococcum (wild/domestic einkorn)

Both one and two-grained einkorn were exploited, cultivated and domesticated in the Neolithic (Table 2 in ESM 2). One-grained einkorn was one of the main cereal species at Tell Qaramel, dated to 12.3–10.8 ka cal BP (Willcox et al. 2008), but clear evidence of cultivation is not found until ca. 10.7–10.2 ka cal BP, when this species showed cultivated-type grain sizes and was predominant at several sites in southeast Turkey (Pasternak 1998; van Zeist and de Roller 1991/1992). Around the same time, one grained-einkorn seemed to have been translocated to Cyprus ca. 10.5–10.1 ka cal BP, as recorded at Mylouthkia (Murray 2003). The evidence of domestication for one-grained einkorn is limited (see Table 2 in ESM 2). At Nevalı Çori, domestic-type rachises constitute only 13.8% of the assemblage, whereas at Çayönü van Zeist and de Roller (1991/1992) argue that all the wheat spikelet forks were domestic-type, but published drawings do not provide clear evidence. Indeed, the material would benefit from re-examination following recent categorizations (Tanno and Willcox 2012; Charles et al. 2021). The evidence for the presence of domestic type one-grained einkorn chaff during the MPPNB is also meagre (see Table 2 in ESM 2), and it is therefore considered that so far, one of the earliest and most convincing cases of domestication for one-grained einkorn is found at Çatalhöyük, where large quantities of both domestic-type grains and chaff remains were recovered dated to ca. 9.1–8.4 ka cal BP (Fairbairn et al. 2002).

The initial exploitation of two-grained einkorn is difficult to trace, as the wild species share some morphological characteristics with wild rye, and in the literature these have been often reported as *Triticum/Secale* (see Table 2 in ESM 2). The initial cultivation of morphologically wild two-grained einkorn could have occurred during the PPNA in the Euphrates, but it never constituted the main crop (van Zeist

and Bakker-Heeres 1982; Willcox et al. 2008). Evidence for two-grained einkorn domestication is found at the EPPNB site of Tell Qarassa North, in the central-southern Levant, where it constituted one of the main cereal taxa alongside emmer (Arranz-Otaegui et al. 2016a, b). However, whether these remains represent two-grained *T. monococcum* or a domesticated but currently extinct form of *T. urartu* is not yet possible to determine. This crop continued to be present at sites dated to ca. 9.8–8.3 ka cal BP (Willcox 2005 and Table 3 in Asouti and Fuller 2013) and it was translocated, possibly as a second wave introduction, to Cyprus ca. 9.5 ka cal BP (Lucas et al. 2012). Fully domesticated two-grained einkorn (i.e. showing > 90% of non-shattering chaff) is attested only during the Chalcolithic period (Willcox 2003; Tanno and Willcox 2006a).

T. dicoccoides/dicoccum (wild/domestic emmer)

Although regarded as a founder species, the presence of emmer during the PPNA is rare overall (see Table 3 in ESM 2), and its deliberate exploitation cannot be inferred until the ca. 10.7–10.2 ka cal BP, at sites such as Tell Qarassa North, where it represented the main cereal crop (Arranz-Otaegui et al. 2016a, b). By ca. 10.7 ka cal BP domesticated-type emmer chaff is recorded in the central Levant (Arranz-Otaegui et al. 2016a, b) and a few centuries later in central Anatolia (Ergun et al. 2018), whereas in Iran, domesticated-type emmer chaff is not found until ca. 9.8 ka cal BP (Riehl et al. 2013). Around 10.8–10.4 ka cal BP emmer is translocated to Cyprus (Murray 2003; Vigne et al. 2012), soon becoming one of the most commonly exploited cereal species across southwest Asia and Europe (Zohary et al. 2012).

Triticum aestivum/durum and *Hordeum var. nudum* (bread wheat, durum wheat and naked barley)

The widespread presence of naked cereals in southwest Asia is recorded around 10 ka cal BP, during the MPPNB, but recent evidence from Anatolia shows that these domesticated species could have been deliberately exploited just few centuries after the development of domestic emmer, ca. 10.4 ka cal BP (Ergun et al. 2018). Free-threshing wheat and barley are later attested in Cyprus ca. 8.5 ka cal BP (Stewart 1974; Waines and Price 1977; Hansen 1994; Parés and Tengberg 2017) and Crete ca. 8.6–8.4 ka cal BP (Colledge and Conolly 2007; Douka et al. 2017). It is overall difficult to distinguish between naked hexaploid and tetraploid wheat in absence of rachis remain and thus the origin and development of naked wheats is still subject of intense debate (see Zohary 1969; Hillman 1978; de Moulins 1997; Özkan et al. 2005; Pozzi and Salamini 2007; Oliveira et al. 2012; Pont et al. 2019). Nevertheless, it is interesting to note that at many PPNB sites, free-threshing cereals are found at higher

proportions than founder species like hulled barley, chickpea, pea and bitter vetch. Moreover, naked cereals, wheat in particular, replaced hulled cereals at several early Neolithic sites in Europe (Zohary et al. 2012; Antolín et al. 2015).

***T. turgidum/timophevii* (the new glume wheat)**

Recent aDNA evidence shows that the previously called ‘new glume wheat’ is indeed a member of the *T. timopheevii* group (Czajkowska et al. 2020). This species may have been domesticated from the *T. timopheevi* ssp. *araticum* (Jones et al. 2021). Some of the earliest records for the new glume wheat come from Aşıklı Höyük ca. 10.4 ka cal BP, where it was cultivated along with emmer and had signs of being in the process of domestication based on the presence of non-shattering rachises (Ergun et al. 2018). This species was also attested slightly later at Cafer Höyük, ca. 10.2 ka cal BP, where it seemed to have been cultivated from the very beginning of the occupation (de Moulins 1997), as well as at Çatalhöyük, where the domestication of new glume wheat was still on going at least during the early and middle phases of the site (Charles et al. 2021). Considering that the identification criteria for this species have been established relatively recently, it is likely that exploitation of the new glume wheat during the Neolithic was more extended than previously thought (Jones et al. 2000; Kohler-Schneider 2003; Bogaard et al. 2013). Although it has been considered a ‘lost crop’, this species spread to Europe, and it is attested in a number of sites as late as the third millennium BP, indicating that its exploitation persisted over millennia (Jones et al. 2000).

***Aegilops* spp., *Taeniatherum caput-medusae*, *Piptatherum holciforme*, *Stipa* spp., cf. *Eragrostis* spp. and *Heterantheium piliferum* (goatgrass, medusahead, rice grass, feathergrass, lovegrass)**

At several early Neolithic sites, dated to ca. 11.6–10 ka cal BP, deliberate exploitation and consumption of small and medium-seeded grasses such as *Aegilops* spp., *Taeniatherum caput-medusae*, *Stipa* sp. and *Piptatherum holciforme* has been suggested based on their high frequencies and the presence of several taphonomic features associated with food processing (Weide et al. 2017, 2018; Whitlam et al. 2018). Weide et al. (2017, 2018) report that goatgrass was one of the main grasses exploited at Chogha Golan 11.7–9.6 ka cal BP, and that it could have represented an important source of food that was under management. Medusahead is another plant that shows counts comparable to the those reported for wild cereals at several PPNA and EPPNB sites in the Euphrates and Turkey, suggesting it was deliberately gathered and possibly consumed (Savard et al. 2006; Willcox et al. 2008; Weide et al. 2017, 2018; Ergun 2018).

Additionally, the Triticoid remains found at several early Neolithic sites in Iran and Iraq, recently identified as a winter annual species of the Triticeae tribe called *Heterantheium piliferum*, could also have been part of the plant-food resources exploited during the early Neolithic in the eastern Fertile Crescent (Weide et al. 2021). Whether these grass species were collected from the wild or could have been subject to management is yet unknown, primarily due to the lack of metrical analyses or close examination of associated chaff remains.

Legumes

The evidence suggests that at least five legume species were under cultivation during the Neolithic, and additional five or six taxa were regularly exploited and could have been under management.

***Lens orientalis/culinaris* (wild/domestic lentil)**

The earliest clear-cut evidence of exploitation of lentils in the Neolithic is attested ca. 12 ka cal BP in northern Syria, at the site of Tell Qaramel (Willcox et al. 2008), and at a number slightly later PPNA and EPPNB sites across the Levant (see Table 4 in ESM 2). The high ubiquity and frequencies attested for this species (sometimes higher than those reported for cereals) could indicate the development of dormancy-free lentil mutants around 11.6–10.7 ka cal BP, as wild lentil is characterised by high seed dormancy and poor yield, meaning that its harvest and cultivation would not have been efficient (Zohary and Hopf 1973; Ladizinsky 1979). Nevertheless, it is traditionally accepted that domesticated lentils developed around 10.2 ka cal BP at sites such as Cafer Höyük, where lentils were present in high amounts, and showed domestic-type seed sizes (de Moulins 1997), and at the broadly contemporary site of Yiftahel (Garfinkel et al. 1988), where 1.4 million lentils were found along with *Galium tricorntutum* (corn cleavers), a weed characteristic of lentil fields. Lentils became one of the key crops that spread to Europe during the Neolithic, as attested at the Aceramic site of Mylouthkia in Cyprus ca. 10.5–10.1 ka cal BP (Murray 2003). However, recent evidence at the multi-period site of Franchthi cave in Greece shows that this species was exploited since the Mesolithic, and it was not incorporated into Neolithic plant-based subsistence (Asouti et al. 2018).

***Pisum elatium/sativum* (wild/domestic pea)**

Pea has been exploited since at least the Late Natufian (Tanno et al. 2013; van Zeist and Bakker Heeres 1984) and the wild species, identified on the basis of its rough testa, is reported at a small number of PPNA and EPPNB sites in the Euphrates (see Willcox et al. 2008, also Table 5 in ESM

2). At Çayönü, sizes of peas dated to ca. 10.6–10.2 ka cal BP were similar to domestic varieties dated to ca. 9.5–9.3 ka cal BP, suggesting they could have constituted cultivars, but rough testa characteristic of wild species were reported (van Zeist and de Roller 1991/1992). Thus, the earliest clear evidence for pea domestication based on the presence of soft testa varieties is reported at Jericho II (Hopf 1983) dated to ca. 10.2–9.9 ka cal BP. Slightly later, by ca. 9.7–9.5 ka cal BP, domestic peas with smooth testa are found at sites in Turkey (Renfrew 1968; van Zeist and Waterbolk-van Rooijen 1985; van Zeist and de Roller 1991/1992). Nevertheless, at Çatalhöyük both wild and domestic peas were exploited (Fairbairn et al. 2002, 2005), and even at later Neolithic sites, such as Hacilar, the presence of wild peas is still attested (Helbaek 1970). Pea was translocated to Cyprus ca. 10.5–10.1 ka cal BP (Murray 2003), and later to other regions in Europe (see Zohary et al. 2012).

***Vicia ervilia* (bitter vetch)**

Bitter vetch was present at a number of Pre-Pottery Neolithic sites starting ca. 11.5 ka cal BP, but except for M'lefaat and Çayönü, its deliberate exploitation cannot be clearly argued for due to the overall low number of finds reported (see Table 6 in ESM 2). Some of the earliest evidence for bitter vetch cultivation, storage and probably also domestication is found at Çayönü, and dates to 9.5–9.3 ka cal BP (van Zeist and de Roller 1991/1992). Here, a deposit containing over 3,800 bitter vetch seeds was found inside a house, indicating that this species was grown for human consumption. Later PPNB and Pottery Neolithic finds are also remarkable. At Çatalhöyük ca. 9.1–8.4 ka cal BP a total of 571 bitter vetch remains were found (Fairbairn et al. 2002), and recent reports indicate the presence of this species in storage contexts (Bogaard et al. 2021). Bitter vetch is documented ca. 9.6–7.8 ka cal BP in Cyprus (Hansen 2005), and ca. 8.4–8.1 ka cal BP at Neolithic sites in Greece (van Zeist and Bottema 1971).

***Cicer reticulatum/arietinum* (wild/domestic chickpea)**

The presence of chickpea is very rare during the Neolithic (see Table 7 in ESM 2). Evidence for chickpea exploitation and possible cultivation is attested at Tell el-Kerkh dated to ca. 10.5–10.3 ka cal BP, where 138 seeds were recovered (Tanno and Willcox 2006b). Chickpeas similar in morphology to the wild progenitor *C. reticulatum* and others that had the characteristics of modern cultivated species were reported at this site (Tanno and Willcox 2006b, p 200). Yet, the so far earliest domesticated forms of chickpea characterised by soft testa are documented at Jericho (II), ca. 10.2–9.5 ka cal BP, and are similar in size to specimens recovered at PPNB and Early Bronze Age sites (Hopf 1983).

As Zohary et al. (2012) noted, this species is rare even at Pottery-Neolithic sites, indicating that chickpea was not a major Neolithic cultivar. Nevertheless, it was introduced to Cyprus ca. 8.5 ka cal BP (Stewart 1974), and its exploitation increased primarily during the Bronze ages (Zohary et al. 2012).

***Vicia faba* (faba bean)**

The earliest evidence for faba bean was found at the late Epipaleolithic site of El Wad (Caracuta et al. 2016), and later on at the PPNA Iraq ed-Dubb, although its identification was tentative (i.e. *Vicia* cf. *faba*-type, Colledge 2001). At the EPPNB Tell el-Kerkh (Tanno and Willcox 2006b), 437 faba bean seeds were recovered, representing one of the largest assemblages dated to this time period. Recent finds show that this species was regularly exploited from 10.2 ka cal BP onwards at sites in Israel, and most likely represented domesticated varieties (Kislev 1985; Caracuta et al. 2015, 2017). At the LPPNB Yiftahel 2750 seeds were recovered in a storage structure dated to ca. 8.8 ka cal BP, suggesting that this species represented a domestic cultivar (Kislev 1985). Around the same time, ca. 8.8 ka cal BP, faba bean was translocated to Cyprus (van Zeist 1981) and subsequently, ca. 7.5 ka cal BP, it appears at Neolithic sites in Europe (Costantini et al. 1997).

***Vicia peregrina* (rambling vetch)**

It has been suggested that rambling vetch was cultivated at the PPNA site of Netiv Hagdud, where 313 seeds were found scattered along with thousands of wild barley grains (Melamed et al. 2008). Nevertheless, not all authors are in agreement with its status as a cultivar (see Abbo et al. 2013), as a detailed study of the associated domestication traits (e.g. seed size, testa etc.) is yet not available.

***Vicia* spp., *Lathyrus* spp. and small/medium-seeded Fabaceae (vetch species, grass pea species and small/medium-seeded legumes)**

It is interesting to note that aside from the founder taxa, the exploitation of several other legume species was practiced during the Pre-Pottery and Pottery Neolithic periods. For example, at the site of Çatalhöyük two pure deposits of *Vicia noeana* (broad-podded vetch), and an indeterminate legume seed, identified as *Lathyrus/Vicia* sp., with a concentration of 126 seeds dominating a sample from an occupation deposit were documented (Helbaek 1964; Fairbairn et al. 2002). In Cyprus, *Vicia narbonensis*-type seeds were reported ca. 8.8–8.1 ka cal BP (van Zeist 1981), indicating that not only founder species were translocated during the Neolithic. In the mainland, *Lathyrus sativus/cicera* (grass

pea/chickling vetch) is attested at several PPNB sites such as Çayönü and Catalhöyük (Kislev 1986; van Zeist and de Roller 1991/1992; Fairbairn et al. 2002), including storage concentrations (Bogaard et al. 2021). Significant finds of ca. 800 seeds were also found at Gritille dated to the final PPNB (Miller 2002). This species is attested along with the traditional founder crops at several Neolithic sites in Greece and Bulgaria (Kislev 1989b; Halstead and Jones 1980). In Ahihud (Israel), *Lathyrus inconspicuus* (inconspicuous pea) was found in similar contexts as other founder legumes, showed the same frequencies as lentil (195 remains) and was even more common than bitter vetch, which was represented by only 36 remains. However, this species, along with *Lathyrus hierosolymitanus* was interpreted as fodder, based on uses attested in modern ethnobotanical studies (Caracuta et al. 2017, yet note that inconspicuous pea is reported as food in other ethnobotanical works; see Rivera Nuñez et al. 2012). This is also the case for most small and medium-seeded legumes (e.g. *Astragalus* sp., *Trigonella* sp., *Melilotus* sp. etc.), the role of which during the Neolithic has been subject to much debate (see Butler 1995). These types of legumes are present since the late Epipalaeolithic, through the PPNA, PPNB and Pottery Neolithic sites (see Table 3.4 and Fig. 3.4 in ESM 1), and according to ethnographic records they could have constituted plant-foods, fodder resources and/or weeds of cultivated crops (see Rivera Nuñez and Obón de Castro 1991; Rivera Nuñez et al. 2012). Small and medium-seeded legumes such as *Trigonella* sp., *Astragalus* sp. (milk vetch) or *Medicago* sp. (medick) were the main legume taxa at least at eight aceramic sites (11.6–10.2 ka cal BP). They showed particularly high frequencies at Chogha Golan (X-XI) and Körtik Tepe (1,737 and 462 remains respectively, Riehl et al. 2013; Rössner et al. 2018). At Tell Aswad (I) more than 400 *Trigonella astroites*-type seeds were recorded, which they clearly outnumbered wild wheat and pea finds (<25 remains, van Zeist and Bakker Heeres 1984). However, whether small and medium-seeded legumes were deliberately exploited and cultivated during the Neolithic has not been sufficiently investigated yet. It may well be that, just as shown by ethnobotanical literature, these plants served indeed for multiple purposes (food, fodder, medicines, sources of gum, soil fertilisers etc. see detailed accounts for multiple species in Rivera Nuñez et al. 2012).

Other potentially managed plant resources

Apart from cereals and pulses, Neolithic communities exploited a wide range of other plant resources, which included at least 19 of the so-called ‘wild plant’ taxa and five fruit-bearing trees and shrubs (see also Wallace et al. 2019).

The ‘wild plants’

Plants other than cereal and legumes have been traditionally interpreted as ‘wild’ gathered plant resources, but we here argue that these plant resources could have also been subject to management practices and consequently, domestication. Indeed, mounting archaeobotanical evidence shows that a number of species of the Brassicaceae, Polygonaceae, Cyperaceae, Amaranthaceae, Malvaceae and Papaveraceae (mustard, buckwheat, sedge, amaranth and poppy families) were intensively exploited during the Neolithic across southwest Asia (see Table 3.1 in ESM 1 and Wallace et al. 2019). It is well-known that during the first part of the Neolithic, ca. 11.6 ka cal BP, human groups in southeast Turkey relied on the exploitation of plants other than the wild progenitors of domesticated cereals (Savard et al. 2006; Kabukcu et al. 2021). The use of genera such as *Scirpus/Bolboschoenus* sp. (club rush, Savard et al. 2006; Douché and Willcox 2018; Rössner et al. 2018; Kabukcu et al. 2021), *Papaver* sp. (poppy, Whitlam et al. 2018), and *Polygonum/Rumex* sp. (knotweed/curly dock Willcox et al. 2008) is well documented across the area. At sites in the Euphrates, the economic use of plants of the mustard family is attested by the presence two ‘cakes’ made of crushed seeds, and the overall high numbers of crucifer seeds found in the non-woody plant assemblages (Willcox 2002; Willcox et al. 2008). Absolute counts for other ‘wild’ taxa such as Caryophyllaceae and Chenopodiaceae (more than 2,491 remains), and aromatic *Ziziphora* sp. (553 remains) indicate that these edible species were recurrently used at Körtik Tepe (Rössner et al. 2018). Interestingly, the exploitation of *Ziziphora* sp. is also documented at broadly contemporary sites in northwest Syria and southeast Turkey (Willcox et al. 2008; Savard et al. 2006). The presence of edible ‘wild plant’ taxa continued to be significant during the PPNB. At Aşıklı Höyük, concentrations of *Papaver cf. rhoeas/dubium* (poppy) seeds, *Camelina* sp. (false flax), *Helianthemum* (rock rose) and *Verbascum* spp. (mullein) fruits were recorded (Ergun 2018). *Helianthemum* is also present with significant counts at broadly contemporary Nevalı Çori, and it could have constituted a source of food (Pasternak 1998). Recent reports from Catalhöyük also indicate that the seeds of this plant were deliberately stored, possibly for consumption, during the LPPNB (Bogaard et al. 2021). At this site, stores of *Capsella bursa-pastoris* (shepherd’s-purse) and *Descurainia sophia* (fixweed) were also found dated to ca. 8.8–8.2 ka cal BP (Bogaard et al. 2005, 2013, 2021; Fairbairn et al. 2007). The analyses of carbonised food remains from the site confirms that Brassicaceae seeds and club-rush tubers were used as food together with a number of cereals and pulses (González-Carretero et al. 2017). The evidence overall indicates that a number of ‘wild plant’ resources were repetitively and quite intensively

exploited during the Neolithic, which opens up the possibility for their cultivation.

In this sense, we consider that flax could have been regarded as an additional plant within the wide range of economically relevant plant resources exploited during the Neolithic (see Table 8 in ESM 2). This species is attested primarily at sites dated to between 10.2–8.5 ka cal BP (Fig. 4), and overall show lower ubiquity and absolute counts than other economically useful ‘wild plant’ taxa (see Table 3 in ESM 1). Nevertheless, it is likely that this species was domesticated during the Neolithic period in southwest Asia. At the MPPNB site of Jericho a flax capsule dated to ca. 9.9 ka cal BP was identified, and the plant was interpreted as a cultivar (Hopf 1983). At the LPPNB site of Tell Ramad in Syria, flax seeds fall within the size of domesticated species (van Zeist and Bakker Heeres 1984), and its spread to Europe is well documented at a number of Neolithic sites (see Fig. 1 in Karg 2011), starting ca. 10.5–10.1 ka cal BP in Cyprus (Murray 2003). Yet, it is interesting to point out that the frequencies of this species in southwest Asia declined significantly with the development of the Pottery Neolithic, ca. 8.5 ka cal BP (Fig. 4).

Management of fruit-bearing trees and shrubs

Zohary et al. (2012, p 115) postulated that *Olea* (olive), *Vitis* (grapevine), *Ficus carica* and *F. sycomorus* (fig and sycamore fig), *Phoenix dactylifera* (date palm) and *Punica granatum* (pomegranate) constituted the earliest fruit trees that were taken into cultivation in southwest Asia and Europe (see also Zohary and Spiegel-Roy 1975; Weiss 2015). But, with the possible exception of fig, which could have been managed during the early Neolithic ca. 11.5 ka cal BP as evidenced at Gilgal I (Kislev et al. 2006; contra Lev-Yadun et al. 2006 and Denham 2007, who argue that the evidence gathered at this site could have resulted from the preferential exploitation of wild and ‘seedless’ female figs), the process of tree cultivation would have taken place after the development of agriculture, during the Chalcolithic-Bronze Age. As a result, fruit bearing trees have been traditionally considered as a ‘second-wave’ of domesticates. Yet, there is no reason to think that cutting and rooting of twigs, digging out of suckers, planting basal knobs or transplanting of shoots were not conducted during the Neolithic. Indeed, the archaeobotanical evidence shows at the time when Neolithic cereal and pulse cultivation practices were developing, taxa such as *Pistacia* spp. (pistachio), *Amygdalus* spp. (almond) and *Capparis* sp. (caper) were recurrently, and often quite intensively exploited across southwest Asia (see Table 3 in ESM 1). Finds from Anatolia show that the use of almond as a source of food had a long tradition that could be traced back to at least to the Epipalaeolithic (Martinoli and Jacomet 2004). Considering that wild almond relatives are commonly

bitter and toxic, processing activities and the selection and propagation of preferred varieties could have been practised in the past. Indeed, the evidence for wood charcoal exploitation in the southern Levant shows the intensive exploitation of both pistachio fruits (Rousou et al. 2021), and wood resources during the PPNA and the PPNB (see review of early Holocene wood charcoal records in southwest Asia in Table S5 in Arranz-Otaegui et al. 2017), and some authors suggest that that this species could have been managed during the Neolithic for the collection of nuts and firewood (Asouti et al. 2015). In addition, *Quercus* spp. (oak) seems to have been recurrently exploited at Çatalhöyük, as evidenced by the presence of acorn stores, and the use of its wood as fuel and building material (Asouti 2013; Bogaard et al. 2013). Indeed, it has also been suggested that semi-arid deciduous oak woodlands in the Irano-Anatolian regions represented anthropogenic vegetation types that evolved during the first half of the Holocene, as a result of human activities like tree coppicing, pollarding and shredding, as well as sheep grazing (Asouti and Kabukcu 2014). However, even if the archaeobotanical record shows that several fruit-bearing trees and shrubs were recurrently exploited during the Neolithic, clear-cut evidence of management and/or cultivation is still missing for the largest part of the period. Similarly, there is not enough data yet to determine whether the fruit-bearing trees/shrubs attested at aceramic sites in Cyprus such as caper, fig and pistachio in the early phases (ca. 10.5–10.1 ka cal BP, Willcox 2001; Murray 2003) and olive, *Celtis* sp. (hackberry), and *Prunus* spp. (plum genus) slightly later ca. 8.4–8.1 ka cal BP (Hansen 2005), were locally available or imported together with the rest of the grain crops from the mainland area.

Discussion

Revisiting the significance of the founder crops

Zohary and Hopf (1988) originally claimed that the founder crops were the “most numerous vegetable remains” at early Neolithic farming villages, and since then, these eight species have become the hallmark of the Neolithic period, leading several authors to suggest that einkorn, emmer, barley, pea, bitter vetch, chickpea and flax represented the original group of plants that were first cultivated and domesticated in southwest Asia, as well as the species that agricultural communities exploited and translocated to other regions (Zohary 1989, 1996; Lev-Yadun et al. 2000; Gopher et al. 2001; Abbo et al. 2012). Yet, these claims can now be empirically re-evaluated through the archaeobotanical data accumulated in the last four decades.

Considering both the ubiquity and absolute values of the different taxa it can be concluded that the eight founder

species were neither the most numerous nor the most common edible plant species attested during the Neolithic in southwest Asia. Archaeobotanical data indicate that early and late Neolithic communities exploited dozens of different edible plant resources and that the particular species selected varied greatly through the period and across the region (see also Savard et al. 2006; Arranz-Otaegui et al. 2016a, b; Wallace et al. 2019). In fact, for the first thousand years of the Neolithic, i.e. 11.6–10.2 ka cal BP, the founder crops were extremely rare; only barley and lentils seem to have been exploited with some regularity. A relative increase in the founder crops is attested during the middle PPNB, 10.2–9.5 ka cal BP, which coincides with the start of the early Neolithic agricultural phase. But the founder species attested during this time only comprised barley, emmer, einkorn, lentil and flax (Fig. 4) along with several other crops (e.g. naked wheat, naked barley, new glume wheat, faba bean, grass pea). It is not until the end of the Pre-Pottery Neolithic, and particularly, during the late Neolithic agricultural phase (i.e. Pottery Neolithic, 8.5 ka cal BP onwards), that founder species increased more significantly and that taxa such as pea and bitter vetch were incorporated (Fig. 4). Yet, even during this late Neolithic agricultural phase, the frequencies for chickpea, pea, bitter vetch and flax continued to be very low in comparison to non-founder taxa such as naked cereals, and other food resources such as fruits and nuts, and the edible ‘wild plants’. Overall, results show that the gradual increase in the exploitation of the founder crops over time is almost entirely explained by the increased presence of wheat in archaeological sites (Fig. 4), and not so much because the eight founder species become predominant over other taxa.

The archaeobotanical data also suggests that the founder crops were not the first group of plants taken under cultivation. According to the information available to date, the first cultivated crops would be attested during the Pre-Pottery Neolithic A (11.6–10.7 ka cal BP). But of the eight founder species, only wild barley and perhaps lentil appear to have been cultivated during this time period. The cultivation of emmer, einkorn, bitter vetch, chickpea, pea and flax is not documented until later, during the PPNB (10.7–9.0 ka cal BP). Indeed, the evidence indicates that early Neolithic plant cultivation activities involved (at least) taxa such as wild rye, and that therefore, the beginning of food production in southwest Asia included species other than the original founder taxa.

Results also show that the eight Neolithic founder crops were not the group of plants first domesticated in southwest Asia. Key domestication traits for the founder cereal and legume species (i.e. non-shattering rachis and smooth testa) are documented from 10.7 to 9.6 ka cal BP. Yet, within this time frame, there is clear-cut evidence for the development of domestication traits for other crops like faba bean ca. 10.7–10.2 ka cal BP, free-threshing cereals and new glume

wheat ca. 10.4 ka cal BP, as well as broad-vetch, grass-pea and other legumes, domesticated between 10.2–9.6 ka cal BP, during the MPPNB and the LPPNB. As such, the idea that the eight founder crops represented the first group of species that underwent domestication during the Neolithic, and that ultimately led to the development of agriculture (*sensu* Lev-Yadun et al. 2000; Gopher et al. 2001; Abbo et al. 2010, 2012), should be discarded.

Actually, it is not even accurate to consider this group of eight plants as the species that ‘founded’ agriculture in southwest Asia. Whilst taxa like barley and emmer, and to a lesser extent einkorn, were recurrently exploited during the whole agricultural period (i.e. MPPNB, 10.2 ka cal BP onwards, Fig. 4), bitter vetch and pea did not become common cultivars until ca. 8.5 ka cal BP, that is, almost one millennium after the development of agriculture (see Fig. 4). The same applies to chickpea, but this taxon remained extremely rare during the whole Neolithic period, including the Pottery Neolithic, which raises the question of why Zohary and Hopf ever regarded this plant as a founder. Indeed, what is clear from the data accumulated in the last 40 years is that aside from the founder species, a large number of crops comprising at least free-threshing wheat, grass pea, faba bean, ‘new’ glume wheat, but probably many more (potentially plants of the mustard family, fruit-bearing trees etc.), were recurrently exploited during the agricultural period. Consequently, it can be argued that not only one, but mostly likely multiple agricultures existed during the Neolithic, each comprising different combinations of cultivars and ‘crop packages’.

Overall, we consider that the focus on the eight founder crops in the literature has inevitably resulted in a stereotyping of Neolithic subsistence (see also Arranz-Otaegui 2021). The plant-based economy of the Neolithic is often portrayed as a rather homogeneous entity, where plant cultivation was the primary activity, and the species targeted were exclusively—or at least primarily—the eight founder species. Yet this widespread view contradicts the archaeobotanical data gathered in the last decades, which shows that the Neolithic was a dynamic period that included multiple plant-based subsistence strategies and the exploitation of many more species than the traditional eight founders (Colledge 2001; Savard et al. 2006; Fairbairn et al. 2007; Willcox et al. 2008; Asouti 2013; Bogaard et al. 2013, 2021; Arranz-Otaegui et al. 2016b; Caracuta et al. 2016, 2017; Baird et al. 2018; Colledge et al. 2018; Douché and Willcox 2018; Ergun 2018; Ergun et al. 2018; Weide et al. 2018; Whitlam et al. 2018; Wallace et al. 2019; Kabukcu et al. 2021).

We know that once an agricultural way of life was fully established, the Neolithic founder crops spread outward in different waves: to the west into Europe; to the north, into the Caucasus and Turkmenistan; and to the east, towards the Iranian Plateau and southern central Asia (see Colledge

et al. 2004; Charles and Bogaard 2010). However, these eight species were taken to other regions, but not necessarily as a clear package. As previously shown, at most Neolithic sites between one and four of the eight founder species are attested along with several other economically useful plant species (Colledge et al. 2004, 2005; Charles and Bogaard 2010; Weiss and Zohary 2011; Asouti and Fuller 2013). Perhaps more importantly, the Neolithic founder species were neither the first nor the only crops that spread from southwest Asia to other regions, and recent archaeobotanical evidence in Cyprus clearly exemplifies this fact. In this island several introductions of plant species are attested during the Neolithic, including: (1) barley and emmer ca. 10.8–10.6 ka cal BP; (2) one-grained einkorn, pea, bitter vetch, flax, oat and perhaps several fruit-bearing trees like caper, fig and pistachio ca. 10.5–10.1 ka cal BP; (3) two-grained einkorn ca. 9.5 ka cal BP; (4) faba bean/narbon vetch ca. 8.8 ka cal BP; and (5) naked barley and wheat, along with chickpea, and probably other taxa like hackberry, olive and plum, slightly later ca. 8.4–8.1 ka cal BP (Stewart 1974; van Zeist 1981; Willcox 2001; Murray 2003; Hansen 2005; Colledge and Conolly 2007; Lucas et al. 2012; Vigne et al. 2012; Parés and Tengberg 2017; Lucas and Fuller 2020).

Taking together the evidence that has accumulated over the last four decades, we can conclude that while the eight species listed by Zohary and Hopf undoubtedly played a relevant economic, cultural and social role during the Neolithic, as well as subsequent prehistoric and historic periods up to the present day, it is misleading to consider these eight plants as the founder species or as a clear package. If it is deemed of use for scientific discussion, the concept of the ‘founder crops’ should at least be revised to include other species (e.g. see previous suggestions by Melamed et al. 2008; Fuller et al. 2011, 2012a, b), as well as to evaluate the suitability of maintaining some of the original taxa (e.g. chickpea). But in our view, it is not enough to merely modify the lists of species. We propose that instead of, or at least in addition to, defining the first cultivars, domesticates, translocated species etc., it could perhaps be more helpful to define the plants that founded the Neolithic subsistence as a whole, irrespective of their form (wild, domestic, intermediate), procurement strategy (cultivated, gathered) and uses (food, fuel, raw materials...). We consider that by so doing, we would be best positioned to compare long-term plant exploitation strategies through direct comparisons with the evidence found in other time periods (e.g. by comparing ‘the plants of the Epipaleolithic subsistence’ v. ‘the plants of the Neolithic subsistence’). The removal of long-established dichotomies (i.e. wild/domestic, crop/gathered plant etc.) would also allow us to evaluate more accurately the relevance of the wide range of different plant species these communities exploited.

Current challenges and future prospects in relation to the study of the origins of agriculture in southwest Asia

Considering the data accumulated in the last decades, it is clear that there are important challenges at both theoretical and methodological levels in our understanding of the origins of agriculture in southwest Asia. Research in plant domestication has primarily focused on tracing the evolutionary history of particular cereal and legume species (see Arranz-Otaegui 2021). As such, there is plenty of work to be done in order to investigate the domestication process of crop species that have not traditionally been included in the founder crop category, but for which there is clear archaeobotanical evidence of cultivation, domestication and translocation during the Neolithic (e.g. rye, naked cereals, new glume wheat, faba bean and grass pea among many others). Yet, perhaps more interestingly, it remains to be investigated whether some of the so-called ‘wild plant’ resources (including the fruit and nut category), underwent management processes during the Neolithic even if they resulted in evolutionary dead ends. In this sense, the archaeobotanical data suggest a number of taxa that would be worth exploring.

In terms of grasses, species like goatgrass, medusahead, featherglass and several other medium and small-seeded grasses were predominant and seemed to have played an important role in the economy of early Neolithic sites in Turkey, Iran and Iraq (Baird et al. 2018; Whitlam et al. 2018; Rössner et al. 2018; see Weide et al. 2018 for a detailed revision for the exploitation of wild grasses in southwest Asia). Indeed, the exploitation of these ‘other’ types of grasses as a source of food dates back at least to the Upper Palaeolithic–Early Epipaleolithic period (Weiss et al. 2004) and continued throughout the Late Epipaleolithic (Hillman 2000; Colledge and Conolly 2010; Tanno et al. 2013; Rössner et al. 2018). The fact that many of these species are edible and have been economically relevant for modern populations as indicated by ethnobotanical accounts (Adams 1999; Rivera Nuñez et al. 2012; Fairbairn et al. 2014;), along with the evidence for the cultivation and domestication of similar small/medium-seeded grasses around the world (e.g. *Eragrostis tef*, *Pannisetum glaucum*, *Panicum/Setaria*, *Echinochloa crus-galli*, *Phalaris caroliniana*, *Hordeum pusillum*), provides solid grounds to open the possibility for their management during the Neolithic in southwest Asia.

The cultivation and domestication process of legumes like rambling vetch, broad-podded vetch and inconspicuous pea could be explored to better understand the economic role that these species played in the subsistence of Neolithic communities in southwest Asia (Melamed et al. 2008; Caracuta et al. 2017). In this sense, it is important to note that some of these taxa appear in larger proportions than founder legumes like chickpea and pea; they have been documented in storage

contexts, just like other founder crop species; and ethnobotanical records show they have been used as food in the past (Rivera Nuñez and Obón de Castro 1991; Rivera Nuñez et al. 2012). This also applies to small-seeded legumes, like milk vetch or medick (see ethnobotanical examples of the economic uses of several species in Rivera Nuñez and Obón de Castro 1991; Rivera Nuñez et al. 2012). It has been considered that small-seeded legumes could have played an important role in terms of subsistence, either as food or fodder, in particular regions like Iran and/or Iraq (Savard et al. 2006; Riehl et al. 2013). Empirical evidence for the cultivation of these species is currently non-existent, and research is constrained by the inherent difficulties associated with the identification of legume domestication, as well as the cultural biases and modern preconceptions behind the potential exploitation of non-founder plants (Arranz-Otaegui 2021). As previously noted by Butler (2009, p 99), “these types of ‘other’ pulse species have been labelled ‘wild’ seemingly because they are not from any of today’s known crops, while ancient pulse crops have been partially so defined by association with known cereal and the modern crops status”.

The cultivation and domestication of plants that belong to families other than the Poaceae and Fabaceae is a possibility that, except for flax and some fruit-tree crops, has been neither seriously considered nor positively explored yet in southwest Asia. Archaeobotanical evidence shows that during the earliest phases of the Neolithic a wide range of resources including plants of the Cyperaceae, Polygonaceae, Chenopodiaceae and Brassicaceae families was exploited in southwest Asia (see also Wallace et al. 2019). Some of these species showed very high frequencies, even higher than founder cereals and legumes, and they were found in storage contexts or large concentrations, just like other cultivated crops (Fairbairn et al. 2002; Willcox 2002; Willcox et al. 2008; Ergun 2018). We know that during prehistory, the cultivation and domestication of plants in the mustard, goosefoot and buckwheat families, among others, occurred in other parts of the world (Bruno 2006; Smith and Yarnell 2009; Mueller 2017; Hunt et al. 2018; see Meyer et al. 2012 for a review). As such, a fundamental question to be tackled in southwest Asia is whether these so-called ‘wild plant’ resources were being managed during the Neolithic period, and whether they also spread from southwest Asia along with the founder cereals and legumes to other regions in the north, south and east.

Finally, it should be noted that landscape and woodland management practices are one of the major gaps in our knowledge of anthropogenic land-uses and plant management activities in southwest Asia. We consider that the overall late empirical records for the management of fruit trees could be primarily a result of our lack of ability to trace these practices archaeologically. Indeed, recent scholarship

is showing that Pleistocene human groups around the world were already managing the land and the plant resources around them through the use of fire and the translocation of plant species (Boivin et al. 2016). Such early land and plant management activities have also been suggested for the Epipalaeolithic period in southwest Asia (Emery-Barbier and Thiébaud 2005; Turner et al. 2010; Ramsey and Rosen 2016). It is therefore one of the key topics that deserves to be further investigated in future archaeobotanical studies, and which would benefit from the application of multiple lines of evidence (e.g. morphometric study of seeds/fruits, dendro-anthracological studies, pollen and micro-charcoal analyses, and plant provenance analyses, among others).

Conclusions

The concept of the ‘founder crops’ developed by Zohary and Hopf represented a before and after in our understanding of the Neolithic plant-based subsistence and the origins of agriculture in southwest Asia. It largely influenced the grand explanatory models for the transition to food production, and shaped our research agendas. But this concept was developed in the 1980s, when processes such as plant cultivation, domestication and agriculture were used interchangeably in the literature. As such, this paper has sought to revisit the significance of the founder crops concept in the light of the archaeobotanical advances carried out in the last decades.

Zohary and Hopf (1988) considered these eight species as the “most numerous vegetable remains in early farming villages”, “the species that initiated food production in southwest Asia”, the first domesticated plants, as well as the crops that founded early Neolithic agriculture and spread from southwest Asia to other regions. In this work we have shown that these definitions are not accurate, and that for each of these key aspects (i.e. plant cultivation, domestication, agriculture, translocation) the list of species that would need to be regarded as ‘founders’ would be significantly different. There is no doubt that individually, species like barley, emmer, lentil and einkorn played a fundamental role during the Neolithic, but results showed that taxa such as flax, pea, bitter vetch and chickpea were not more common than other economically useful plant species. Overall, we consider that our knowledge about plant domestication and the development of agriculture is retrospective, and it has been largely biased by modern views and expectations of past subsistence practices and agriculture (Arranz-Otaegui 2021). Just as it has been argued for when reflecting on the very nature of the Neolithic “by looking for this long-established and recognized suite of traits that form a Neolithic ‘package’ we tend to ignore the diversity from which these features emerge, a

diversity that appears to be a central part of the transition” (Finlayson 2013, p 133).

This paper has also highlighted current gaps and existing limitations in our knowledge about Neolithic plant exploitation. There has been (and continues to be) a clear underestimation of the role that non-founder plant taxa played during this time. In our view, the narratives of Neolithic subsistence, the process of domestication, and development and spread of agriculture in southwest Asia cannot be limited to the evolution of these eight taxa alone. We therefore propose that in order to move our understanding of the Neolithic plant-based subsistence and agriculture forward, we have to raise new questions like: Which of the many exploited plant species were under management during the Neolithic? Could some of the so-called ‘wild plant’ taxa be cultivated too? Did some of these species ever become domesticated? Could we trace their spread to other regions?

Overall, if the same amount of time, effort and interest invested in documenting the domestication process of the founder crops was applied to identify the evolutionary history of other plant species, our knowledge about the transition from foraging to plant-food production in southwest Asia would have been much more comprehensive and factual than at present, and we would therefore be better positioned to understand the origins and development of this fundamental process.

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Declarations

Conflict of interest The authors declare no competing interests.

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References

- Abbo S, Gopher A (2020) Plant domestication in the Neolithic Near East: the humans-plants liaison. *Quat Sci Rev* 242:106412
- Abbo S, Gopher A, Rubin B, Lev-Yadun S (2005) On the origin of Near Eastern founder crops and the “dump-heap hypothesis.” *Genet Resour Crop Evol* 52:491–495. <https://doi.org/10.1007/s10722-004-7069-x>
- Abbo S, Gopher A, Peleg Z et al (2006) The ripples of “The Big (agricultural) Bang”: the spread of early wheat cultivation. *Genome* 49:861–863
- Abbo S, Lev-Yadun S, Gopher A (2010) Agricultural origins: centers and noncenters; a Near Eastern reappraisal. *Crit Rev Plant Sci* 29:317–328
- Abbo S, Lev-Yadun S, Gopher A (2012) Plant domestication and crop evolution in the Near East: on events and processes. *Crit Rev Plant Sci* 31:241–257
- Abbo S, Lev-Yadun S, Heun M, Gopher A (2013) On the “lost” crops of the Neolithic Near East. *J Exp Bot* 64:815–822
- Adams KR (1999) Macrobotanical remains. In: Varien MD (ed) *The Sand Canyon archaeological project: site testing (Version 1.0, CD-ROM)*. Crow Canyon Archaeological Center, Cortez
- Antolín F, Jacomet S, Buxó R (2015) The hard knock life. Archaeobotanical data on farming practices during the Neolithic (5400–2300 cal BC) in the NE of the Iberian Peninsula. *J Archaeol Sci* 61:90–104
- Arranz-Otaegui A (2015) Beyond vegetation and plant food production, exploring wood gathering strategies, crop husbandry and plant use at Tell Qarassa North (south Syria). Unpublished PhD thesis, University of the Basque Country (UPV-EHU), Leioa, Spain
- Arranz-Otaegui A (2021) Archaeology of plant foods: methods and challenges on the identification of plant-foods during the Pre-Pottery Neolithic in southwest Asia. *Food Hist* 19:79–109
- Arranz-Otaegui A, Colledge S, Zapata L, Teira-Mayolini LC, Ibáñez JJ (2016a) Regional diversity on the timing for the initial appearance of cereal cultivation and domestication in southwest Asia. *Proc Natl Acad Sci USA* 113:14001–14006
- Arranz-Otaegui A, Colledge S, Ibáñez JJ, Zapata L (2016b) Crop husbandry activities and wild plant gathering, use and consumption at the EPPNB Tell Qarassa North (south Syria). *Veget Hist Archaeobot* 25:629–645
- Arranz-Otaegui A, López-Sáez JA, Araus JL, Portillo M, Balbo A, Iriarte E, Gourichon L, Braemer F, Zapata L, Ibáñez JJ (2017). *Quat Sci Rev* 158:145–163 Landscape transformations at the dawn of agriculture in southern Syria (10.7–9.9 ka cal. BP): plant-specific responses to the impact of human activities and climate change
- Arranz-Otaegui A, González Carretero L, Roe J, Richter T (2018a) “Founder crops” v. wild plants: assessing the plant-based diet

- of the last hunter-gatherers in southwest Asia. *Quat Sci Rev* 186:263–283
- Arranz-Otaegui A, González Carretero L, Ramsey M, Fuller DQ, Richter T (2018b) Archaeobotanical evidence reveals the origins of bread 14,400 years ago in northeastern Jordan. *Proc Natl Acad Sci USA* 115:7925–7930
- Asouti E (2013) Woodland vegetation, firewood management and woodcrafts at Neolithic Çatalhöyük. In: Hodder I (ed) *Humans and landscapes of Çatalhöyük: reports from the 2000–2008 seasons*. Cotsen Institute of Archaeology Press, Los Angeles, pp 129–162
- Asouti E, Fuller DQ (2013) A contextual approach to the emergence of agriculture in Southwest Asia. *Reconstructing Early Neolithic plant-food production*. *Curr Anthropol* 54:299–345
- Asouti E, Kabukcu C (2014) Holocene semi-arid oak woodlands in the Irano-Anatolian region of Southwest Asia: natural or anthropogenic? *Quat Sci Rev* 90:158–182
- Asouti E, Kabukcu C, White CE et al (2015) Early Holocene woodland vegetation and human impacts in the arid zone of the southern Levant. *Holocene* 25:1565–1580
- Asouti E, Ntinou M, Kabukcu C (2018) The impact of environmental change on Palaeolithic and Mesolithic plant use and the transition to agriculture at Franchthi Cave, Greece. *PLoS ONE* 13:e0207805. <https://doi.org/10.1371/journal.pone.0207805>
- Baird D, Fairbairn A, Jenkins E et al (2018) Agricultural origins on the Anatolian plateau. *Proc Natl Acad Sci USA* 115:E3077–E3086. <https://doi.org/10.1073/pnas.1800163115>
- Bogaard A, Jones G, Charles M (2005) The impact of crop processing on the reconstruction of crop sowing time and cultivation intensity from archaeobotanical weed evidence. *Veget Hist and Archaeobot* 14:505–509
- Bogaard A, Charles M, Livarda A et al (2013) The archaeobotany of mid-later Neolithic occupation levels at Çatalhöyük. In: Hodder I (ed) *Humans and landscapes of Çatalhöyük: reports from the 2000–2008 Seasons*. Cotsen Institute of Archaeology Press, Los Angeles, pp 93–128
- Bogaard A, Charles M, Filipovic D, Fuller DQ, González Carretero L, Green L, Kabukcu C, Stroud E, Vaiglova P (2021) The archaeobotany of Çatalhöyük: results from 2009–2017 excavations and final synthesis. In: Hodder I (ed) *Peopling the landscape of Çatalhöyük: reports from the 2009–2017 Seasons*. Çatalhöyük Research Project Series 13. British Institute at Ankara, London, pp 91–123
- Boivin NL, Zeder MA, Fuller DQ et al (2016) Ecological consequences of human niche construction: examining long-term anthropogenic shaping of global species distributions. *Proc Natl Acad Sci USA* 113:6388–6396
- Bruno MC (2006) A morphological approach to documenting the domestication of *Chenopodium* in the Andes. In: Zeder MA, Bradley D, Emswiler E, Smith BD (eds) *Documenting domestication: new genetic and archaeological paradigms*. University of California Press, Berkeley, pp 32–45
- Butler A (1995) The small-seeded legumes: an enigmatic prehistoric resource. *Acta Palaeobot* 35:105–115
- Butler A (2009) Evidence of domestication in the Old World grain legumes. In: Fairbairn AS, Weiss E (eds) *From foragers to farmers: papers in honour of Gordon C. Oxbow Books*, Oxford, Hillman, pp 98–102
- Caracuta V, Barzilai O, Khalaily H et al (2015) The onset of faba bean farming in the Southern Levant. *Sci Rep* 5:14370
- Caracuta V, Weinsten-Evron M, Kaufmann D et al (2016) 14,000-year-old seeds indicate the Levantine origin of the lost progenitor of faba bean. *Sci Rep* 6:37399. <https://doi.org/10.1038/srep37399>
- Caracuta V, Vardi J, Paz Y, Boaretto E (2017) Farming legumes in the pre-pottery Neolithic: New discoveries from the site of Ahihud (Israel). *PLoS ONE* 12:e0177859. <https://doi.org/10.1371/journal.pone.0177859>
- Charles M, Bogaard A (2010) Charred plant macro-remains from Jeitun: implications for early cultivation and herding practices in western Central Asia. In: Harris DR (ed) *Origins of agriculture in Western Central Asia: an environmental-archaeological study*. University of Pennsylvania Museum of Archaeology and Anthropology, Philadelphia, pp 150–165
- Charles M, Fuller DQ, Roushannafas T, Bogaard A (2021) An assessment of crop plant domestication traits at Çatalhöyük. In: Hodder I (ed) *Humans and Environments of Çatalhöyük: reports from the 2009–2017 seasons*. British Institute at Ankara, London, pp 125–136
- Colledge S (2001) Plant exploitation on Epipalaeolithic and early Neolithic sites in the Levant. *BAR International Series* 986. BAR Publishing, Oxford
- Colledge S, Conolly J (2007) A review and synthesis of the evidence for the origins of farming on Cyprus and Crete. In: Colledge S, Conolly J (eds) *The origins and spread of domestic plants in Southwest Asia and Europe*. Left Coast Press, Walnut Creek, pp 53–74
- Colledge S, Conolly J (2010) Reassessing the evidence for the cultivation of wild crops during the Younger Dryas at Tell Abu Hureyra, Syria. *Environ Archaeol* 15:124–138
- Colledge S, Conolly J, Shennan S (2004) Archaeobotanical evidence for the spread of farming in the eastern Mediterranean. *Curr Anthropol* 45:S35–S58
- Colledge S, Conolly J, Shennan S (2005) The evolution of Neolithic farming from SW Asian origins to NW European limits. *Eur J Archaeol* 8:137–156
- Colledge S, Conolly J, Finlayson B, Kuijt I (2018) New insights on plant domestication, production intensification, and food storage; the archaeobotanical evidence from PPNA Dhra'. *Levant* 50:14–31. <https://doi.org/10.1080/00758914.2018.1424746>
- Costantini L, Costantini-Biasini L, Lentini A (1997) Agricoltura e note sull'ambiente dell'abitato Neolitico di Scamuso. In: Biancofiore F, Coppola D (eds) *Scamuso: per la storia delle comunità umane tra il VI ed il III millennio nel basso Adriatico*. Dipartimento di Storia dell'Università di Roma "Tor Vergata", Paletnologia, Roma, pp 199–209
- Czajkowska BI, Bogaard A, Charles M et al (2020) Ancient DNA typing indicates that the “new” glume wheat of early Eurasian agriculture is a cultivated member of the *Triticum timopheevii* group. *J Archaeol Sci* 123:105258
- De Moulins D (1997) Agricultural changes at Euphrates and steppe sites in the mid-8th to the 6th millennium B.C. *BAR International Series* 683. BAR Publishing, Oxford
- Denham T (2007) Early fig domestication, or gathering of wild parthenocarpic figs? *Antiquity* 81:457–461
- Douché C, Willcox G (2018) New archaeobotanical data from the Early Neolithic sites of Dja'de el-Mughara and Tell Aswad (Syria): a comparison between the northern and the southern Levant. *Paléorient* 44:45–58
- Douché C, Willcox G (2023) Identification and exploitation of wild rye (*Secale* spp.) during the early Neolithic in the Middle Euphrates valley. *Veget Hist Archaeobot*. <https://doi.org/10.1007/s00334-023-00906-4>
- Douka K, Efstratiou N, Hald MM, Henriksen PS, Karetso A (2017) Dating Knossos and the arrival of the earliest Neolithic in the southern Aegean. *Antiquity* 91:304–321
- Edwards PC, Meadows J, Sayej G, Westaway M (2004) From the PPNA to the PPNB: new views from the southern Levant after excavations at Zahrat adh-Dhra' 2 in Jordan. *Paléorient* 30:21–60
- Emery-Barbier A, Thiébaud S (2005) Preliminary conclusions on the Late Glacial vegetation in south-west Anatolia (Turkey): the

- complementary nature of palynological and anthracological approaches. *J Archaeol Sci* 32:1,232–1,251
- Ergun M (2018) “Where the wild things are”. Contextual insights into wild plant exploitation at Aceramic Neolithic Aşıklı Höyük. *Turkey Paléorient* 44:9–28
- Ergun M, Tengberg M, Willcox G, Douché C (2018) Plants of Aşıklı Höyük and changes through time: first archaeobotanical results from the 2010–14 excavation seasons. In: Özbaşaran M, Duru G, Stiner M (eds) *The early settlement at Aşıklı Höyük. Essays in Honor of Ufuk Esin*. Ege Yayınları, İstanbul, pp 191–218
- Fairbairn AS (2019) Revision for the crop history of aceramic Neolithic Canhasan III, Karaman, Turkey. 18th IWGP abstract book. Università del Salento, Lecce
- Fairbairn A, Asouti E, Near J, Martinoli D (2002) Macro-botanical evidence for plant use at Neolithic Çatalhöyük south-central Anatolia, Turkey. *Veget Hist Archaeobot* 11:41–54
- Fairbairn A, Near N, Martinoli D (2005) Macrobotanical Investigation of the North, South and KOPAL area excavations at Çatalhöyük East. In: Hodder I (ed) *Inhabiting Çatalhöyük: reports from the 1995–99 seasons*. BIAA Monographs Series 38. British Institute at Ankara, London, pp 137–201
- Fairbairn A, Martinoli D, Butler A, Hillman G (2007) Wild plant seed storage at Neolithic Çatalhöyük East, Turkey. *Veget Hist Archaeobot* 16:467–479
- Fairbairn AS, Jenkins E, Baird D, Jacobsen G (2014) 9th millennium plant subsistence in the central Anatolian highlands: new evidence from Pınarbaşı, Karaman Province, central Anatolia. *J Archaeol Sci* 41:801–812
- Finlayson B (2013) Imposing the Neolithic on the past. *Levant* 45:133–148
- Fuller DQ (2007) Contrasting patterns in crop domestication and domestication rates: recent archaeobotanical insights from Old World. *Ann Bot* 100:903–924
- Fuller DQ, Willcox G, Allaby RG (2011) Cultivation and domestication had multiple origins: arguments against the core area hypothesis for the origins of agriculture in the Near East. *World Archaeol* 43:628–652
- Fuller DQ, Asouti E, Purugganan MD (2012a) Cultivation as slow evolutionary entanglement: comparative data on rate and sequence of domestication. *Veget Hist Archaeobot* 21:131–145
- Fuller DQ, Willcox G, Allaby RG (2012b) Early agricultural pathways: moving outside the ‘core area’ hypothesis in Southwest Asia. *J Experiment Bot* 63:617–633
- Fuller DQ, Lucas L, González Carretero L, Stevens C (2018) From intermediate economies to agriculture: trends in wild food use, domestication and cultivation among early villages in Southwest Asia. *Paléorient* 44:59–74
- Garfinkel Y, Kislev ME, Zohary D (1988) Lentil in the Pre-Pottery Neolithic B Yiftah’el: additional evidence of its early domestication. *Isr J Bot* 37:49–51
- González Carretero L, Wollstonecroft M, Fuller DQ (2017) A methodological approach to the study of archaeological cereal meals: a case study at Çatalhöyük East (Turkey). *Veget Hist Archaeobot* 26:415–432. <https://doi.org/10.1007/s00334-017-0602-6>
- Gopher A, Abbo S, Lev-Yadun S (2001) The “when”, the “where” and the “why” of the Neolithic revolution in the Levant. *Doc Praehist* 28:49–62
- Gyulai F (2014) Archaeobotanical overview of rye (*Secale Cereale* L.) in the Carpathian-Basin I. from the beginning until the Roman Age. *Columella: J Agric Environ Sci* 1:25–36
- Halstead P, Jones G (1980) Early Neolithic economy in Thessaly: some evidence from excavations at Prodromos. *Anthropologika* 1:93–117
- Hammer K (1984) Das Domestikationssyndrom Die Kulturpflanze 32:11–34
- Hansen J (1994) Khirokitia plant remains: preliminary report (1986, 1988–1990). In: le Brun A (ed) *Fouilles récentes à Khirokitia (Chypre), 1988–1990*. Editions Recherche sur les Civilisations, Paris, pp 393–409
- Hansen J (2005) Flora. In: Todd IA (ed) *Vasilikos valley project 1: the bronze age cemetery in Kalavassos Village*. Paul Åströms Förlag, Sävedalen, pp 323–341
- Harris DR (1996) Introduction: themes and concepts in the study of early agriculture. In: Harris DR (ed) *The origins and spread of agriculture and pastoralism in Eurasia*. UCL Press, London, pp 1–9
- Harris DR, Fuller DQ (2014) Agriculture: definition and overview. In: Smith C (ed) *Encyclopedia of global archaeology*. Springer, New York, pp 104–113
- Helbaek H (1964) First impressions of the Çatal Hüyük plant husbandry. *Anatol Stud* 14:121–123
- Helbaek H (1970) The plant husbandry of Hacilar. In: Mellaart J (ed) *Excavations at Hacilar*. Edinburgh University Press, Edinburgh, pp 189–244
- Heun M, Schäfer-Pregl R, Klawan D et al (1997) Site of einkorn wheat domestication identified by DNA fingerprinting. *Science* 278:1,312–1,314
- Hillman G (1978) On the origins of domestic rye - *Secale Cereale*: the finds from Aceramic Can Hassan III in Turkey. *Anatol Stud* 28:157–174
- Hillman GC (2000) The economy of the two settlements at Abu Hureyra. In: Moore AMT, Hillman GC, Legge AJ (eds) *Village on the Euphrates: from foraging to farming at Abu Hureyra*. Oxford University Press, Oxford, pp 327–398
- Hillman CG, Davies MS (1990) Domestication rates in wild-type wheats and barley under primitive cultivation. *Biol J Linn Soc* 39:39–78
- Hopf M (1983) Appendix B: Jericho plant remains. In: Kenyon KM, Holland TA (eds) *Excavations at Jericho, vol 5. The pottery phases of the tell and other finds*. British School of Archaeology in Jerusalem, London, pp 576–621
- Hunt HV, Shang X, Jones MK (2018) Buckwheat: a crop from outside the major Chinese domestication centres? A review of the archaeobotanical, palynological and genetic evidence. *Veget Hist Archaeobot* 27:493–506
- Jones G, Valamoti S, Charles M (2000) Early crop diversity: a “new” glume wheat from northern Greece. *Veget Hist Archaeobot* 9:133–146
- Jones G, Kluyver T, Preece C et al (2021) The origins of agriculture: intentions and consequences. *J Archaeol Sci* 125:105290
- Kabukcu C, Asouti E, Pöllath N, Peters J, Karul N (2021) Pathways to plant domestication in southeast Anatolia based on new data from aceramic Neolithic Gusir Höyük. *Sci Rep* 11:2112. <https://doi.org/10.1038/s41598-021-81757-9>
- Karg S (2011) New research on the cultural history of the useful plant *Linum usitatissimum* L. (flax), a resource for food and textiles for 8,000 years. *Veget Hist Archaeobot* 20:507–508
- Kilian B, Özkan H, Walther A, Kohl J, Dagan T, Salamini F, Martin W (2007) Molecular diversity at 18 loci in 321 wild and 92 domesticate lines reveal no reduction of nucleotide diversity during *Triticum monococcum* (einkorn) domestication: implications for the origin of agriculture. *Mol Biol Evol* 24:2657–2668
- Kislev ME (1985) Early Neolithic horsebean from Yiftah’el, Israel. *Science* 228:319–320
- Kislev ME (1986) Archaeobotanical findings on the origins of *Lathyrus sativus* and *L. cicero*. In: Kaul AK, Combes D (eds) *Lathyrus and Lathyrism*. Third World Medical Research Foundation, New York, pp 46–51

- Kislev ME (1989a) Pre-domesticated cereal in the pre-pottery Neolithic A. In: Hershkovitz I (ed) *People and culture in change*. BAR International Series 508. Oxford, pp 147–151
- Kislev ME (1989b) Origins of the cultivation of *Lathyrus sativus* and *L. cicero* (Fabaceae). *Econ Bot* 43:262–270
- Kislev ME, Hartmann A, Bar-Yosef O (2006) Early domesticated fig in the Jordan Valley. *Science* 312:1372–1374
- Kohler-Schneider M (2003) Contents of a storage pit from late Bronze Age Stillfried, Austria: another record of the “new” glume wheat. *Veget Hist Archaeobot* 12:105–111
- Kyllo M (1982) The botanical remains. In: Peltenburg EJ (ed) *Vrysi, a subterranean settlement in Cyprus: excavations at prehistoric Ayios Epiktitos Vrysi 1969–1973*. Aris and Phillips, Warminster, pp 90–93
- Ladizinsky G (1979) The origin of lentil and its wild genepool. *Euphytica* 28:179–187
- Ladizinsky G, Adler A (1976) The origin of chickpea *Cicer arietinum* L. *Euphytica* 25:211–217
- Lev-Yadun S, Gopher A, Abbo S (2000) The cradle of agriculture. *Science* 288:1602–1603
- Lev-Yadun S, Ne’eman G, Abbo S, Flaishman MA, (2006) Comment on “early domesticated fig in the Jordan valley.” *Science* 314:1683
- Lucas L, Fuller DQ (2018) From intermediate economies to agriculture: trends in wild food use, domestication and cultivation among early villages in Southwest Asia. Dataset. UCL Institute of Archaeology. <https://discovery.ucl.ac.uk/id/eprint/10052960/>
- Lucas L, Fuller DQ (2020) Against the grain: long-term patterns in agricultural production in prehistoric Cyprus. *J World Prehist* 33:233–266
- Lucas L, Colledge S, Simmons A, Fuller DQ (2012) Crop introduction and accelerated island evolution: archaeobotanical evidence from ‘*Ais Yiorkis* and Pre-Pottery Neolithic Cyprus. *Veget Hist Archaeobot* 21:117–129
- Luo M-C, Yang Z-L, You FM et al (2007) The structure of wild and domesticated emmer wheat populations, gene flow between them, and the site of emmer domestication. *Theor Appl Genet* 114:947–959
- Martinoli D, Jacomet S (2004) Identifying endocarp remains and exploring their use at Epipaleolithic Öküzini in southwest Anatolia, Turkey. *Veget Hist Archaeobot* 14:45–54
- Melamed Y, Plitzmann U, Kislev ME (2008) *Vicia peregrina*: an edible early Neolithic legume. *Veget Hist Archaeobot* 17:29–34
- Meyer RS, DuVal AE, Jensen HR (2012) Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *New Phytol* 196:29–48
- Miller NF (2002) Tracing the development of the agropastoral economy in southeastern Anatolia and Northern Syria. In: Cappers RTJ, Bottema S (eds) *The dawn of Farming in the Near East. Studies in Early Near Eastern Production, Subsistence, and Environment 6*. Ex Oriente, Berlin, pp 85–94
- Mori N, Ishii T, Ishido T et al (2003) Origins of domesticated emmer and common wheat inferred from chloroplast DNA fingerprinting. In: Pogna NE, Romano M, Pogna EA, Galterio G (eds) *Proceedings of the 10th international wheat genetics symposium, Paestum, Italy*. Istituto Sperimentale per la Cerealicoltura, Rome, pp 25–28
- Mueller N (2017) Documenting domestication in a lost crops (*Polygonum erectum* L.): evolutionary bet-hedges under cultivation. *Veget Hist Archaeobot* 26:313–327
- Murray MA (2003) The plant remains. In: Peltenburg EJ (ed) *The colonisation and settlement of Cyprus: Investigations at Kissonerga-Mylouthkia 1976–1996*. Paul Åströms Förlag, Sävedalen, pp 59–71
- Oliveira HR, Campana MG, Jones H et al (2012) Tetraploid wheat landraces in the Mediterranean Basin: taxonomy, evolution and genetic diversity. *PLoS ONE* 7:e37063. <https://doi.org/10.1371/journal.pone.0037063>
- Özkan H, Brandolini A, Pozzi C et al (2005) A reconsideration of the domestication geography of tetraploid wheats. *Theor Appl Genet* 110:1052–1060
- Özkan H, Willcox G, Graner A, Salamini F, Kilian B (2011) Geographic distribution and domestication of wild emmer wheat (*Triticum dicoccoides*). *Genet Resour Crop Evol* 58:11–53
- Parés A, Tengberg M (2017) Étude des pratiques d’exploitation et d’utilisation des ressources végétales du village de Khirokitia (Chypre) au Néolithique précéramique récent chypriote (VIIe-VIe millénaires av. J.-C.). In: Vigne J-D, Brioso F, Tengberg M (eds) *Nouvelles données sur les débuts du néolithique à Chypre*. Société préhistorique française, Paris, pp 241–251
- Pasternak R (1998) Investigation of botanical remains from Nevalı Çori, PPNB, Turkey: a short interim report. In: Damania AB, Valkoun J, Willcox G, Qualset CO (eds) *The origins of agriculture and crop domestication: The Harlan Symposium*. International Center for Agricultural Research in Dry Areas, Aleppo, pp 170–177
- Pont C, Leroy T, Seidel M et al (2019) Tracing the ancestry of modern bread wheats. *Nat Genet* 51:905–911
- Popper VS (1988) Selecting quantitative measurements in paleoethnobotany. In: Hastorf CA, Popper VS (eds) *Current paleoethnobotany*. University of Chicago Press, Chicago and London, Analytical methods and cultural interpretations of archaeological plant remains, pp 53–71
- Pozzi C, Salamini F (2007) Genomics of wheat domestication. In: Varshney R, Tuberosa R (eds) *Genomic assisted crop improvement, vol 2*. Genomics Applications in Crops. Springer, New York, pp 453–481
- Ramsey MN, Rosen AM (2016) Wedded to wetlands: exploring late pleistocene plant-use in the Eastern Levant. *Quat Int* 396:5–19
- Renfrew J (1968) A note on the Neolithic grain from Can Hasan. *Anatol Stud* 18:55–56
- Riehl S, Kümmel C (2005) Archaeobotanical database of Eastern Mediterranean and Near Eastern Sites (ADEMNES). <https://www.ademnes.de/>
- Riehl S, Zeidi M, Conard NJ (2013) Emergence of agriculture in the foothills of the Zagros Mountains of Iran. *Science* 341:65–67
- Rivera Nuñez D, Obón de Castro C (1991) *La guía de INCAFO de las plantas útiles y venenosas de la Península Ibérica y Baleares (Excluidas medicinales)*. INCAFO, Madrid
- Rivera Nuñez D, Séiquer Matilla G, Obón de Castro C, Alcaraz Ariza FJ (2012) Plants and humans in the Near East and the Caucasus: ancient traditional uses of plants as food and medicine: an diachronic ethnobotanical review. *Ediciones de la Universidad de Murcia, Murcia*
- Rössner C, Deckers K, Benz M, Özkaya V, Riehl S (2018) Subsistence strategies and vegetation development at Aceramic Neolithic Körtik Tepe, southeastern Anatolia, Turkey. *Veget Hist Archaeobot* 27:15–29
- Rousou M, Parés A, Douché C, Ergun M, Tengberg M (2021) Identification of archaeobotanical *Pistacia* L. fruit remains: implications for our knowledge on past distribution and use in prehistoric Cyprus. *Veget Hist Archaeobot* 30:623–639
- Savard M, Nesbitt M, Jones MK (2006) The role of wild grasses in subsistence and sedentism: new evidence from the northern Fertile Crescent. *World Archaeol* 38:179–196
- Shennan SJ, Conolly J (2007) The origin and spread of Neolithic plant economies in the near East and Europe. *Archaeology Data Service*. <https://doi.org/10.5284/1000093>
- Smith BD, Yarnell RA (2009) Initial formation of an indigenous crop complex in eastern North America at 3800 B.P. *Proc Natl Acad Sci USA* 106:6561–6566

- Snir A, Nadel D, Groman-Yaroslavski I et al (2015) The origin of cultivation and proto-weeds, long before Neolithic farming. *PLoS ONE* 10:e0131422. <https://doi.org/10.1371/journal.pone.0131422>
- Stewart R (1974) Paleobotanic investigation: 1972 Season. In: Stager LE, Walker A, Wright GE (eds) American expedition to Idalion, Cyprus: first preliminary report: Seasons of 1971 and 1972. The American Schools of Oriental Research, Cambridge, MA, pp 123–129
- Tanno K, Willcox G (2006a) How fast was wild wheat domesticated? *Science* 311(1):886
- Tanno K, Willcox G (2006b) The origins of cultivation of *Cicer arietinum* L. and *Vicia faba* L.: early finds from Tell el-Kerkh, north west Syria, late 10th millennium B.P. *Veget Hist Archaeobot* 15:197–204
- Tanno K, Willcox G (2012) Distinguishing wild and domestic wheat and barley spikelets from early Holocene sites in the Near East. *Veget Hist Archaeobot* 21:107–115
- Tanno K, Willcox G, Muhesen S et al (2013) Preliminary results from analyses of charred plant remains from a burnt Natufian building at Dederiyeh Cave in northwest Syria. In: Bar-Yosef O, Valla FR (eds) Natufian foragers in the Levant: terminal pleistocene social changes in Western Asia. International monographs in prehistory archaeological series 19. International Monographs in Prehistory, Ann Arbor, Michigan, pp 83–87
- Turner R, Roberts N, Eastwood WJ, Jenkins E, Rosen A (2010) Fire, climate and the origins of agriculture: micro-charcoal records of biomass burning during the last glacial-interglacial transition in Southwest Asia. *J Quat Sci* 25:371–386
- Van Zeist W (1981) Plant remains from Cape Andreas-Kastros (Cyprus). In: Le Brun A (ed) Un site néolithique précéramique en Chypre: Cap Andreas-Kastros. A.D.P.F, Paris, pp 95–99
- Van Zeist W, Bakker-Heeres JAH (1982) Archaeobotanical studies in the Levant 1. Neolithic sites in the Damascus Basin: Aswad, Ghoraife. *Ramad Palaeohistoria* 24:165–256
- Van Zeist W, Bakker-Heeres JAH (1984) Archaeobotanical studies in the Levant 3. Late Palaeolithic Mureybet Palaeohistoria 26:171–199
- Van Zeist W, Bottema S (1971) Plant husbandry in Early Neolithic Nea Nikomedeia, Greece. *Acta Bot Neerl* 20:524–538
- Van Zeist W, de Roller GJ (1991/1992) The plant husbandry of aceramic Çayönü, SE Turkey. *Palaeohistoria* 33/34:65–96
- Van Zeist W, Waterbolk-van Rooijen W (1985) The palaeobotany of Tell Bouqras, eastern Syria. *Paléorient* 11:131–147
- Vigne J-D, Briois F, Zazzo A et al (2012) First wave of cultivators spread to Cyprus at least 10,600 y ago. *Proc Natl Acad Sci USA* 109:8,445–8,449
- Wallace M, Livarda A, Charles M, Jones G (2018) Origins of agriculture: archaeobotanical database. *Archaeology Data Service*. <https://doi.org/10.5284/1046750>
- Wallace M, Jones G, Charles M et al (2019) Re-analysis of archaeological remains from pre- and early agricultural sites provides no evidence for a narrowing of the wild plant food spectrum during the origins of agriculture in southwest Asia. *Veget Hist Archaeobot* 28:449–463
- Waines JG, Stanley Price NP (1977) Plant remains from Khirokitia in Cyprus. *Paléorient* 5:281–284
- Weide A, Riehl S, Zeidi M, Conard NJ (2017) Reconstructing subsistence practices: taphonomic constraints and the interpretation of wild plant remains at aceramic Neolithic Chogha Golan. *Iran Veget Hist Archaeobot* 26:487–504
- Weide A, Riehl S, Zeidi M, Conard NJ (2018) A systematic review of wild grass exploitation in relation to emerging cereal cultivation throughout the Epipalaeolithic and aceramic Neolithic of the Fertile Crescent. *PLoS ONE* 13:e0189811. <https://doi.org/10.1371/journal.pone.0189811>
- Weide A, Arranz-Otaegui A, Schmidt AF, Kim H, Charles M, Zeidi M, Darabi H, Richter T, Conard NJ (2021) Identification of the Triticoid-type grains (Poaceae) from archaeobotanical assemblages in southwest Asia as *Heteranthelium piliferum* (Banks & Sol.) Hochst. *Veget Hist Archaeobot* 30:657–674. <https://doi.org/10.1007/s00334-020-00822-x>
- Weide A, Green L, Hodgson JG, Douché C, Tengberg M, Whitlam J, Dovrat G, Osem Y, Bogaard A (2022) A new functional ecological model reveals the nature of early plant management in southwest Asia. *Nat Plants* 8:623–634. <https://doi.org/10.1038/s41477-022-01161-7>
- Weiss E (2015) “Beginning of fruit growing in the old world”—two generations later. *Isr J Plant Sci* 62:75–85
- Weiss E, Zohary D (2011) The Neolithic Southwest Asian Founder Crops: their biology and archaeobotany. *Curr Anthropol* 52(Suppl 4):S237–S254
- Weiss E, Kislev ME, Simchoni O, Nadel D (2004) Small-grained wild grasses as staple food at the 23,000-year-old site of Ohalo II. *Israel Econ Bot* 58(Suppl):S125–S134
- Weiss E, Kislev ME, Hartmann A (2006) Autonomous cultivation before domestication. *Science* 312:1608–1610
- Whitlam J, Bogaard A, Matthews R, Matthews W, Mohammadifar Y, Ilkhani H, Charles M (2018) Pre-agricultural plant management in the uplands of the central Zagros: the archaeobotanical evidence from Sheikh-e Abad. *Veget Hist Archaeobot* 27:817–831. <https://doi.org/10.1007/s00334-018-0675-x>
- Willcox G (2001) Présence des céréales dans le Néolithique précéramique de Shillourokambos à Chypre: résultats de la campagne 1999. *Paléorient* 26:129–135
- Willcox G (2002) Charred plant remains from a 10th millennium B.P. kitchen at Jerf el Ahmar (Syria). *Veget Hist Archaeobot* 11:55–60
- Willcox G (2003) Chalcolithic carbonised cereals from Ubaid burnt storage structures at Kosak Shamali. In: Nishiaki Y, Matsutani T (eds) Tell Kosak Shamali, vol II. The Archaeological Investigations on the Upper Euphrates. Syria. The University Museum, The University of Tokyo, Tokyo, pp 267–270
- Willcox G (2004) Measuring grain size and identifying Near Eastern cereal domestication: evidence from the Euphrates valley. *J Archaeol Sci* 31:145–150
- Willcox G (2005) The distribution, natural habitats and availability of wild cereals in relation to their domestication in the Near East: multiple events, multiple centres. *Veget Hist Archaeobot* 14:534–541
- Willcox G (2008) Nouvelles données archéobotaniques de Mureybet et la néolithisation du moyen Euphrate. In: Ibañez JJ (ed) Le site néolithique de Tell Mureybet (Syrie du Nord), en hommage à Jacques Cauvin. BAR International Series 1843. BAR Publishing, Oxford, pp 103–114
- Willcox G, Stordeur D (2012) Large-scale cereal processing before domestication during the tenth millennium cal BC in northern Syria. *Antiquity* 86:99–114
- Willcox G, Fornite S, Herveux L (2008) Early Holocene cultivation before domestication in northern Syria. *Veget Hist Archaeobot* 17:313–325
- Zohary D (1969) The progenitors of wheat and barley in relation to domestication and agriculture dispersal in the Old World. In: Ucko PJ, Dumbleby GW (eds) The domestication and exploitation of plants and animals. Duckworth, London, pp 47–66
- Zohary D (1989) Domestication of the Southwest Asian Neolithic crop assemblages of cereals, pulses, and flax: the evidence from the living plants. In: Harris DR, Hillman GC (eds) Foraging and Farming: the evolution of plant exploitation. Unwin & Hyman, London, pp 358–373
- Zohary D (1996) The mode of domestication of the founder crops of Southwest Asian agriculture. In: Harris DR (ed) The origins and

spread of agriculture and pastoralism in Eurasia. Smithsonian Institution Press, Washington DC, pp 142–158

Zohary D, Hopf M (1973) Domestication of pulses in the Old World. *Science* 182:887–894

Zohary D, Hopf M (1988) Domestication of plants in the Old World: the origin and spread of cultivated in west Asia, Europe and the Nive Valley, 1st edn. Clarendon Press, Oxford

Zohary D, Spiegel-Roy P (1975) Beginnings of fruit growing in the Old World. *Science* 187:319–327

Zohary D, Hopf M, Weiss E (2012) Domestication of plants in the Old World, 4th edn. Oxford University Press, Oxford

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