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RESEARCH

Contrasting pathways to domestication and agriculture around Southwest Asia

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Abstract

It has become increasingly apparent that the origins of agriculture in Southwest Asia were an emergent and extended process that resulted from local evolutionary processes and social networks of interaction and exchange that extended across the region. Although the end of the process of domestication and economic transformation shows general regional similarities, sub-regional trajectories differ when evidence of economy and domestication processes are examined independently. This research evaluates the presumed linear trajectory, from hunting and gathering to pre-domestication cultivation to domestication with agriculture and explores the mosaic of subsistence practices leading to agricultural reliance. This paper compiles quantitative data on the proportion of crops in archaeobotanical sites over time and across the Near East. Foraging-focused, mixed subsistence and agricultural economies are compared alongside non-shattering data from cereals with the results suggestive of sites with higher levels of food production (agriculture) without domesticated crops, low-levels of food production with domesticated crops, and variability of economic systems when crops were under pre-domestication cultivation. Results show a dominance of mixed-subsistence economic systems and the persistence of "middle ground societies" for nearly 4,000 years, contradicting ethnographic inferences that intermediate or mixed-subsistence economies are unstable. The potential correlation between reliance on cultivation and domestication, as quantified from morphological evidence for non-shattering or grain size change, indicates that there is not a single directional trend in economy and domestication. There also appears to be some evidence for intensification of the reliance on cultivation as domesticated sheep/goat become widespread. These data highlight the need to consider economic trajectories on different sites and regions independently from the evidence for morphological change.

Keywords Fertile crescent · Neolithic · Pre-domestication cultivation · Archaeobotany · Sheep/goat husbandry · Non-analogue societies

Introduction: the importance of identifying mixed-subsistence economies

The accumulation of archaeobotanical data over recent years has led to increasing evidence that the domestication process was protracted, taking dozens to hundreds of human generations instead of just a few (Tanno and Willcox 2006a; Fuller 2007; Fuller et al. 2014, 2022). This has been accompanied by increasing discussion of the likelihood that Western Asian agricultural origins were non-centric or multi-centric (Gebel 2004; Willcox 2005; Fuller et al. 2011; Arranz-Otaegui et al. 2016a; Ibanez et al. 2018; Özdoğun 2024). As we have come to better understand some of the underlying genetics behind domestication, it is also possible to posit that domestication results from the bringing together of a range of traits, and dozens of gene loci, that have their origins in different populations. This implies that some human populations were using plants and cultivating in ways that selected for some, but perhaps not all, domestication traits; over time gene flow, facilitated through human mobility and trade, brought favourable mutations from different populations together over a period of some millennia (Allaby et al. 2022a, b). In other words, it is not so much that the

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domestication process in southwest Asia was multi-centric, with a few isolated areas of domestication and innovation, but rather that domestication was an emergent process at a regional level that resulted from local evolutionary processes and social networks of interaction and exchange. This chimes with the arguments of the late Andrew Sherratt (2007) that the "neolithic package", including farming, livestock and sedentism, emerged through interaction and exchange amongst early cultivators (especially in the "Levantine corridor") and "climax foragers" in the "hilly flanks" region (see also, Graeber and Wengrow 2021: 233–247). In short, there was no Neolithic or agricultural *revolution* either in terms of the transformation of crop plants or the transformation of societies. This change did not occur concentrated in time nor in space but rather resulted from many different local shifts, in practices and in plant adaptations, that came to be bundled together at the end of the processes of domestication and economic transformation.

There has been a tendency to try to fit the Neolithic transformation process into a linear trajectory, from hunting and gathering to pre-domestication cultivation to domestication with agriculture (e.g., Davies and Hillman 1992; Harris 1996), or via a period of low-level food production that preceded domestication and agriculture (e.g., Smith 2001). In the present contribution we will pick apart such trajectories and argue that it is fundamental to consider separately changes in the human economic systems (non-food production, low-level food production, higher levels of food production) from changes in the plants (domesticated, pre-domestication but cultivated, wild gathered). While these processes are interlinked, they are not identical, and only by keeping them separate can we unravel the regional variation of the mosaic that underpins the emergent properties of domestication. We have previously used the concept of an "Intermediate Economy" after David Harris' (2012) "intermediate subsistence systems." Here we propose to use the less-loaded term *mixed-subsistence* instead, and contrast this with *foraging-focused* on the one side and *crop-dominated* or *agricultural* on the other side. We build upon and improve our previous effort to explore the spectrum of plant economies (Fuller et al. 2018), with an aim of highlighting the existence of higher levels of food production (crop-dominated) without domesticated crops and low-levels of food production (foraging-focused) with domesticated crops present, and a great deal of variability of economic systems during the era when crops were under pre-domestication cultivation. To understand how such processes work, both in terms of biological evolution of crops and cultural histories of practices, we need to frame our evidence clearly and distinguish between mixed-subsistence (or low-level food production, sensu Smith 2001)—a state of cultural practice—and pre-domestication cultivation (PDC), conceived in terms of plant ecology and population genetics (Davies and Hillman 1992; Harris 1996). Smith's (2001) exploration of "low-level food production" (LLFP) highlighted the need to explore a middle ground that escaped the dualistic contrast between foraging and agriculture, domesticated and wild, but quantitative archaeological data for mapping regional timelines across this middle ground was not available at that time. As a result there has been a tendency to conflate pre-domestication cultivation (the evolutionary process in the plant) and economic changes (the degree of reliance on food production). Analytically it is essential to separate these and assess empirically on a case-by-case basis the correlation. Thus, one can explore the relative importance of the persistence of low-level food production while species are undergoing morphological evolution, the extent of low-level food production with fully domesticated cultivars, or high levels of economic reliance (high-level food production) on undomesticated or semi-domesticated crops.

In the present paper, while we refer to LLFP, we prefer to think in terms of mixed-subsistence rather than intermediate economies as we have previously defined (Fuller et al. 2018). Rather than the somewhat arbitrary and difficult to document 50% of diet threshold (suggested by Smith 2001), we now define a foraging-focused economy as less than 25% crops *in archaeological assemblages* and a *crop-dominated* economy when crops account for > 75% on average. In between (25%−75%) crops (or probable crops) we recognize an economy of mixed subsistence. We focus on those plants (cereals, pulses, flax) that are known to have domesticated forms by the end of the Neolithic in the Near East, so there is a basis for assuming that early cultivation began earlier in our period of interest. For other species that might have been managed, or "auditioned" as crops (e.g. *Vicia peregrina, Avena sterilis*, various other grasses, e.g. Weiss et al. 2006; Melamed et al. 2008; Whitlam et al. 2018), we exclude them as further evidence is needed to confirm their cultivation and because they appear to be local to specific sites rather than contributing to wider, long-term regional patterns. We agree with calls for taking a careful look at what species beyond the founder crops may have been managed or cultivated during earlier periods (e.g. Whitlam et al. 2018; Weide et al. 2018; Arranz-Otaegui et al. 2024), but the present paper instead aims to chart variation in economic reliance on cultivation of known crops and how this maps in time and space and relates to biological domestication timelines. Our work extends previous analyses (e.g. Arranz-Otaegui et al. 2018; Fuller et al. 2018) that have drawn attention to the gradual rise in "founder crop" taxa after the Epipalaeolithic, through analysis of a longer time span (ca. 12,500 BC to 5200 BC) on larger, quantitatively robust assemblages, with the aim of characterizing the variable reliance on crops of those species that ultimately emerged as crops.

We recognize that our division of economies into quartiles (< 25%, > 75%, 25–75%) is somewhat arbitrary, but it provides a heuristic starting point. Previously (Fuller et al. 2018), we divided economies into three categories: < 20%, 20–80%, and > 80%. This division emerged from the data themselves, as a histogram of the distribution of percentages across the dataset considered below shows two minima around 20–25% and 75–80% (Fig. S1). Archaeobotanists will argue over what 25% cereals and pulses in a charred assemblage represents in terms of diet, but it is nevertheless quite distinct from the very low quantities that are typically associated with earlier sites, such as in the Epi-Palaeolithic, or the very high levels of cereals that are typical of later periods (Chalcolithic, Bronze Age, and beyond). While 80% was adopted as the minimum for an agricultural economy in an initial study of the southwest Asian data (Fuller et al. 2018), we use 75% here as this simplifies the analysis of archaeobotanical datasets into statistical quartiles. These redefined dividing lines of 25% and 75% are arbitrary but provide a baseline for exploring patterns, and they are a numerical approximation for the impressionistic categories, "very little", "significant amounts", and "a lot". The point here is less about the arbitrary divisions than it is to try to assess when communities or regional cultures were shifting to more agriculturally reliant subsistence practices in economic terms. To what extent did this take place before or after the archaeobiological evidence for domestication, incipient and entrenched pre-domestication cultivation? To what extent did it take place before or after cultivated plants were translocated beyond the geographical limits of their original wild ranges?

The existence of mixed-subsistence economies, how common they were and how long they persisted is theoretically important. It has often been theorized that such systems should not exist or could not persist for very long because they are inherently unstable. This has been argued in the European context to explain the revolutionary, as opposed to gradual, nature of the spread of farming (Rowley-Conwy 2004), and it has more generally been taken by Bellwood (2005, 2013) to bolster the claim that transitions to agriculture were very rare, with most cases being brought about by immigrations of farmers. Smith (2001: 25) already has questioned the reliability of this ethnographically derived framework, arguing that even though they are few and far between, "historically documented in-between societies that have sustained nonagricultural economies right up to into the historic period … representing shining examples of alternative pathways and alternative long-term stable solutions." They may be rare in the present but are not unimportant, and many more examples can probably be sought archaeologically, as "most of the world's middle-ground societies have already been replaced by, or retooled into, agriculturalists" (Smith 2001: 33). Based on ethnographic data (compiled from 862 societies in Murdock's ethnographic atlas), economies tended to be either foraging-based with little or no dietary intake from cultivation (< 10%) or largely food producing with more than 50% of intake from cultivation (Fig. 1). The precise correlation of ethnographic dietary estimates to the equivalent archaeobotanical signature is unclear, but as a starting point we will equate those wild diets (up to 10%) with archaeobotanical assemblages of up to 25% crop remains. This is reasonable given that not all plant components of diet with survive into the archaeobotanical assemblage, which is biased towards hard seeds, nutshell, etc., and thus seed crops like cereals and pulses will be somewhat over-represented compared to some wild foods that are more vegetative in nature. To the proponents of this ethnographic analogical framework for the Neolithic, the economies in-between (Rowley-Conwy's "transitional phase") really should not exist or were extremely rare or are so unstable as to be brief and rarely survive for long-enough to be recovered archaeologically. Bulbeck (2013) has already questioned this through source criticism of Murdock's original data and some recalculation of the ethnography-derived numbers, concluding the lower percentages of agriculture were possible, but still there is a gulf ethnographically between wild-focused and cultivated-majority diets. But there is also a more general empirical

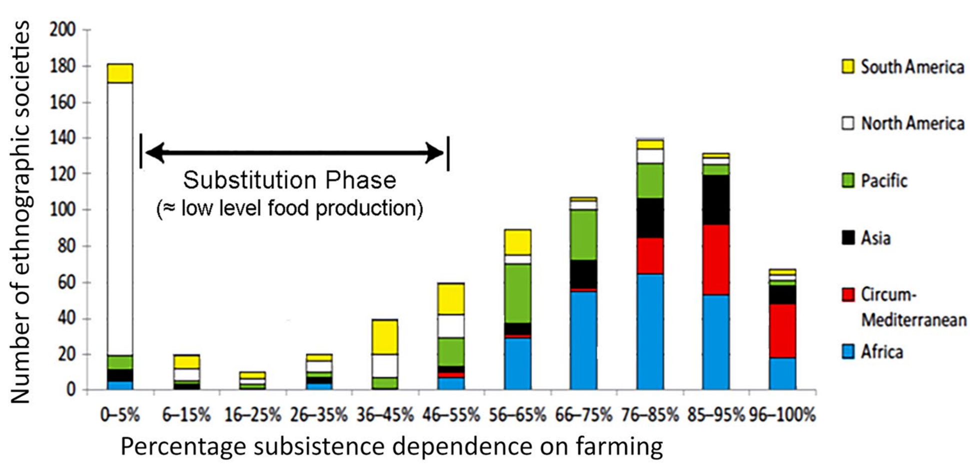

Fig. 1 The representation of farming versus foraging in terms of subsistence dependence based on ethnographic estimates. Chart after Bulbeck (2013) with substitution phase added after Rowley-Conwy (2004). The substitution phase (5%−55% dependence on farming) is nearly equivalent to the Low-Level Food Production concept of up to 50% caloric dependence on cultivation (Smith 2001)

issue: what does the archaeological data suggest? We can ask whether the ethnographic record is a reliable guide to all that might be found archaeologically, including those periods when initial domestication was taking place.

If the ethnographic record is a guide to all significant patterns in the past, then we should expect limited or short-lived evidence for mixed-subsistence systems. Figure 2 is a schematic of what we ought to expect to find archaeobotanically if we follow the logic drawn from aggregated ethnographic data. Other studies, however, have already pointed out that patterns are obscured by such aggregate datasets. Denham and Donohue (2022) have explored the ethnographic atlas for "middle ground" societies that invest at least 15% of their time both in cultivation and in gathering. They found that most of these middle ground societies ethnographically occurred in the tropics of Africa, New Guinea and the Neotropics, as well as in the North American Mississippi basin and the American Southwest. Among these the majority have economies focused on vegeculture or arboriculture, and many fewer with cereal-based cultivation. Those ethnographic mixed-subsistence economies with cereals and pseudo-cereals, are mainly in the New World, leading Denham and Donohue (2022: 8) to suggest that the importance of domesticated ungulates intensified the commitment to cereal cultivation as "crops provide fodder for animals and animals provide manure for fields". This suggests another question to explore which is the extent to which Neolithic sites produce more evidence for crops when they also have increased commitment to pastoral production, generally dated as being established in the Middle Pre-Pottery Neolithic B (PPNB) (8200–7500 BC); but with variation across sites and across the southwest Asian region (Peters et al. 2005; Arbuckle and Atici 2013; Arbuckle and Hammer 2019). The data we gather below allows us to test the hypotheses that (1) the middle ground was unstable and should have few archaeological examples (Fig. 2); (2) that alternatively there were non-analogue socioeconomic systems (as already postulated by Asouti and Fairbairn 2010; Asouti and Fuller 2013) that do not fit with the expectations from the much more shallow time-depth of ethnographic records; and (3) that the adoption of herd animals (sheep, goat, or cattle) had a major intensifying effect on the degree of commitment to cultivation and the emergence of agricultural economies.

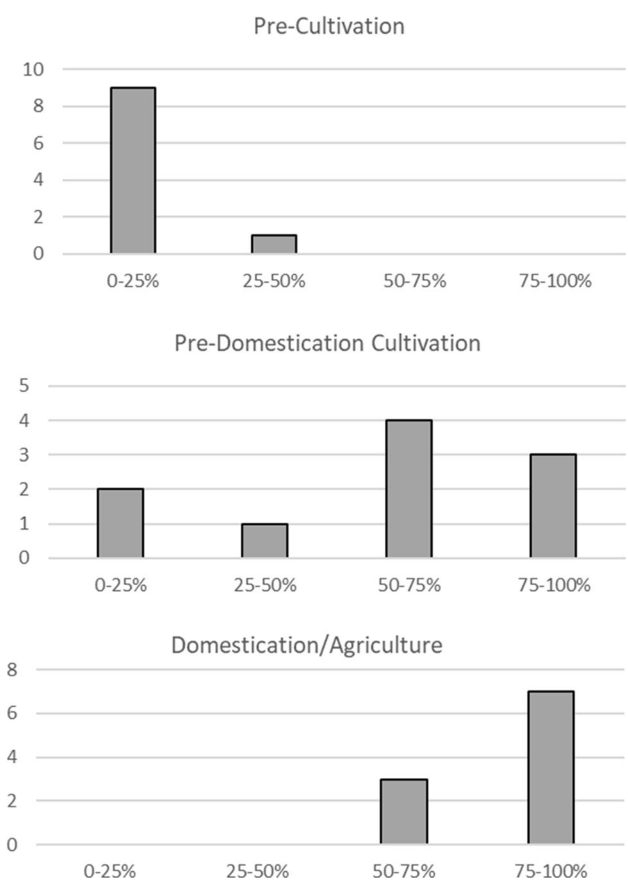

Fig. 2 A schematic of what we might expect to find archaeobotanically in terms of the percentage of crops in assemblages if the data from the ethnographic atlas is used as a guide (as per Rowly-Conwy 2004; Bellwood 2005, 2013). The hypothetical transitional structure during Pre-Domestication Cultivation would therefore be the expectation for the southwest Asian Pre-Pottery Neolithic A or Early Pre-Pottery Neolithic B

Defining cultivation and agriculture, as distinct from domestication

Domestication and the origins of agriculture are both evolutionary processes, and although interconnected they are different. In a strict biological sense, domestication is the evolution of adaptations (phenotypic changes) that make a plant suited to the cultivated environments, or an animal adapted to be herded. Domestication is about plant evolution. Certainly, this evolution is in response to selection created by human activities (cultivation), which selected for rare genetic traits in wild populations or traits that arose by rare mutations that came to be favoured under cultivation. This domestication episode, usually a few millennia, is also often identified by archaeobotanists as "pre-domestication cultivation" (e.g., Davies and Hillman 1992; Harris 1996). While "pre-domestication cultivation" indicates cultivation practices, it rather emphasises the genetic (and morphological) status of the plant. Pre-domestication cultivation is *not the same* as "low-level food production". It could be part of low-level food production or intermediate economies, but it may also be part of wild-focused systems, a small part of foraging economies, and it also could be a component of agricultural economies. In order to clarify the potential intersections between the domestication status of a plant (the degree

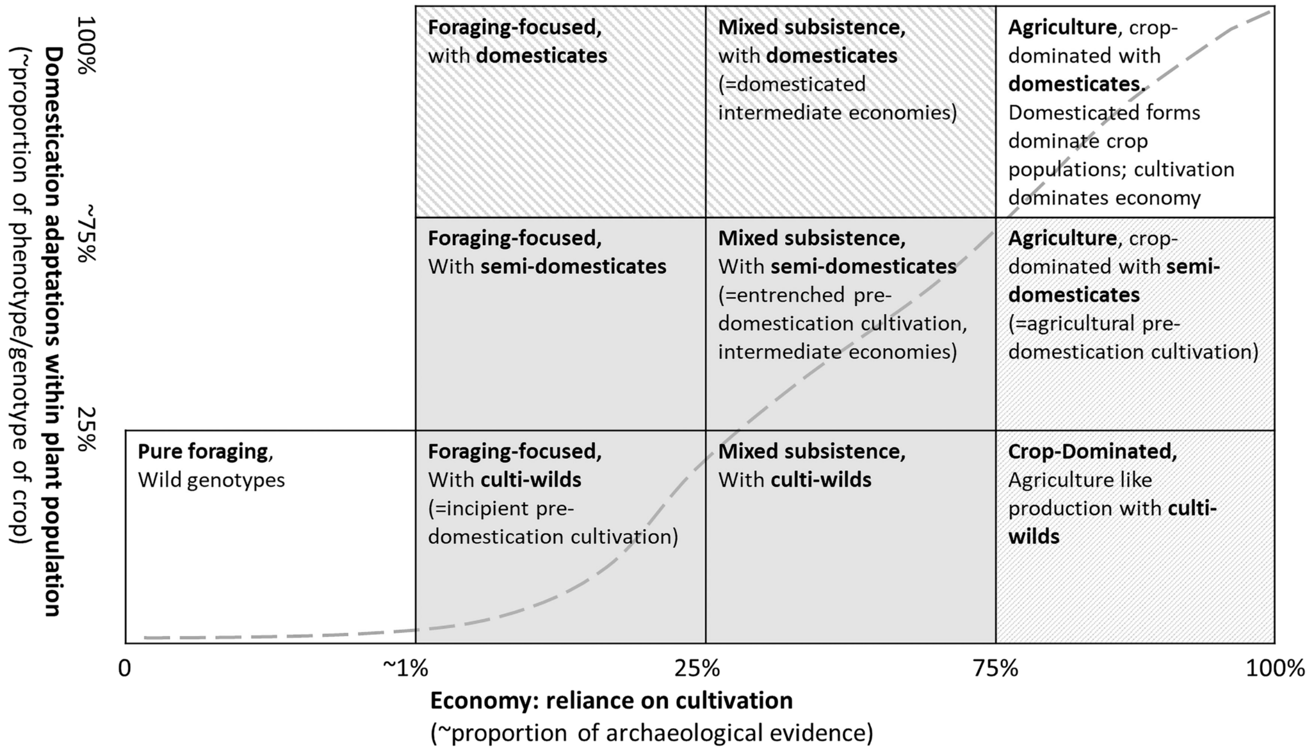

Fig. 3 A matrix of subsistence-domestication states based on the proportion of cultivation in the economies and domestication adaptations in the plant population. The area in solid grey represents conventional "pre-domestication cultivation" systems, while the dashed line indicates the idealised trajectory that has often been assumed, including "incipient" and "entrenched" phases of pre-domestication cultivation. Hatched squares represent systems that have rarely been explicitly recognized ethnographically or archaeologically

of genetic change at a population level) and the degree of economic change, we can define a quantitative matrix based on these two variables with more specific, descriptive terminologies, than the conventional usage of "pre-domestication cultivation" or "low-level food production" (Fig. 3). One can conceive crop-dominated (agricultural-like) economies with large wild-type or semi-domesticated crop populations, or the presence of domesticates in foraging dominant economies. What is important is to keep distinct the plant status and the economic system and explore their inter-relationship empirically.

Domestication can be recognized by archaeobotanical evidence for features that have evolved in parallel across different crop domestications. The domestication syndrome for cereals, and other grain crops, grown from seed and for seed, is well known (Harlan et al. 1973; Fuller 2007; Jones et al. 2021). These characteristics can be related to different aspects of cultivation in terms of what causes them to evolve, including traits related to the establishment of seedlings in cleared soils (competitive selection), while on the other hand there are features that relate human harvesting and sowing cycles (environmental selection) (Allaby et al. 2022a, b). In the present paper we use the evidence of such changes to define a "domestication episode" timeline against which to compare changes in the economy. The nature of archaeobotanical evidence provides two traits of the domestication syndrome to be documented: seed size, which is available for cereals and pulses, and percentage non-shattering (loss of seed dispersal), which is available only for the cereals. Non-shattering is a qualitative trait that distinguishes domesticated plants but evolved as a percentage of plants within a population (Davies and Hillman 1992; Willcox 2024). It is estimated as a percentage within an archaeobotanical assemblage, with the expectation that an original wild population approaches 0% non-shattering, whereas domesticated populations, after evolving under cultivation, approach 100% non-shattering. This is driven by the fact that non-shattering plants will retain more of their seeds when harvested, by a range of methods targeting near-mature grains, and thus contribute a growing proportion to the next sowing (Davies and Hillman 1992; Willcox 2024). For seed size there is no fixed upper limit (equivalent to 100% non-shattering) and thus the extent of change must be deduced from the archaeobotanical record. Previous compilations of size of the Near Eastern cereals indicate that average size and upper limits start to have recognizable increases shortly before or at the same period that non-shattering begins to appear (Willcox 2004; Fuller et al. 2014, 2017, 2023), and that size increases slow down and level off some millennia later: for the wheats and barley the period of most marked change took place from 9500 BC up to to a levelling off around 6000 BC. Pulses also increase in size during the same period, but may be faster and stop increasing sooner (Fuller et al. 2014, 2018). The end of this process then appears to be later than fixation of non-shattering (by at least 1000 years in the Near East), indicating that seed size evolved for longer and at a somewhat slower rate. Evidence on the Chinese millets, *Panicum miliaceum* and *Setaria italica* (Stevens et al. 2021, 2024) or African pearl millet (*Pennisetum glaucum*) (Fuller et al. 2021), suggest the grain sizes continued to increase subsequent to the fixation of non-shattering by as much as 2000 years or more. Increases in size can be compared across taxa by converting assemblage means into a percentage increase over the average of earlier assemblages (Fuller et al. 2018; Fuller and Stevens 2019); this in turn allows the size change trajectory to be broken into phases based on approximate thresholds in percentage change of the mean.

Agriculture is about cultural evolution and change in human behaviour by which the economy becomes increasingly or mostly reliant on cultivated food resources, which are themselves usually domesticated. Domestication is underpinned by genetic changes in the plant (or animal), while agriculture is underpinned by changes in cultural knowledge, practices, and traditions. As already hinted at here and discussed at length elsewhere (e.g., Harris and Fuller 2014; Fuller et al. 2010, 2018), we draw a fundamental distinction between cultivation and agriculture. Both things are activities people do, but while all agriculture (of plants) involves cultivation, not all cultivation is agriculture; agriculture is a matter of scale and degree of dependence whereas cultivation may be small-scale.

It has become evident over the past 20 years that the period over which domestication traits evolved was millennia. Perhaps at least 2000 years for non-shattering, whilst grain size change often continued even longer (e.g., 4000 years) (Fuller et al. 2014, 2018; Stevens et al. 2021). We assume that mixtures of shattering and non-shattering genotypes in the archaeological record reflect mixtures of genotypes in the populations people were harvesting in the past, and can be treated as reflecting the general state of a regional population. Willcox (2024) has also offered an alternative interpretation that such mixtures represent the result of separate harvests from separate wild (shattering) and domesticated (non-shattering populations); however, unless we assume that people could restrict gene flow between these populations, store them separately, avoid sowing from both harvests, and maintain this separation for centuries, these would ultimately become admixed and thus one population. For the purposes of comparing across domestication examples or for contextualizing this process with potential social and ecological factors, it is useful to sub-divide or periodize domestication. While Harris (1996) clearly defined the significance of pre-domestication cultivation we have recently suggested that we should sub-divide it in two stages, incipient and entrenched pre-domestication cultivation, followed by "full" domestication (Fuller et al. 2018; Fuller and Denham 2021). While this is a useful way of breaking up the domestication process analytically for considering cultural and economic correlates, in the current paper we want to move beyond this. The problem is that the concept of pre-domestication cultivation conflates two independent trajectories of change, change in the plant population (domestication) and change in cultural practices (cultivation). Thus in the current study we will define three phases in the evolution of domesticates as follows:

- **Culti-wilds** are plant populations represented by a small minority of morphological domesticates, including up to 25% non-shattering rachises in cereals, and mean seed size increase of up to 10%, in either cereals or pulses. For cereals rachis data are given priority when available. We adapt this term from the literature on vegecultural domestication, such as that of bananas (*Musa*) and tuber crops (De Langhe et al. 2009; Denham et al. 2020). (This is equivalent to incipient pre-domestication cultivation [IPDC] of Fuller et al. 2018. We also considered, but rejected, the term "pro-domestic," long in use by some zooarchaeologists, e.g. Dyson 1953; Meadow 1984.)
- **Semi-domesticates** are plant populations that are in the middle two quartiles of change, which in terms of non-shattering rachises are between 25 to 75%. When rachis data are not available, including for pulse crops, we place assemblages that have mean seed size increases of 10%–30%. (This is equivalent to entrenched pre-domestication cultivation [EPDC] of Fuller et al. 2018.)
- **Domesticates** are taken as plant populations that are in the upper quartile of change. This means a proportion of at least 75% non-shattering rachises and/or > 30% increase in average crop seed size. (This is equivalent to domesticated cultivation [DC] of Fuller et al. 2018.)

These phases do not have hard fixed boundaries but represent grades along a continuum, but for analytical purposes we divide the continuum into these stages (lower quartile, middle quartiles, upper quartile). Fuller and Denham (2021) suggest that the transition of incipient to entrenched pre-domestication may correlate with a shift in emphasis from returns on units of time spent on gathering/harvesting to returns on units of land cultivated. Different communities from the same period may occupy different places in this schema: thus, this generalized schema should not be simplistically considered as a chronological framework. For example, it would be misleading to equate the Pre-Pottery Neolithic A (PPNA) with culti-wilds (or IPDC), the Middle

Pre-Pottery Neolithic B (MPPNB) with semi-domesticates (or EPDC) and the Late Pre-Pottery Neolithic (LPPN) as having only domesticates, as not all crops necessarily evolved in synchronicity nor were all sites of a given period necessarily characterized as having plants at the same level of domestication, nor the same economic system. Instead, it is precisely such diversity that we will explore empirically in the current paper.

Materials and methods

The data and methodology used in this research are an extension of the authors' previously published research (Maeda et al. 2016; Fuller et al. 2018; Lucas and Fuller 2020), but updated to account for new data, constructive reviews, and reliance on larger, more robust assemblage data. It involves the compilation of published archaeobotanical, and radiocarbon data published from primarily two databases, OWCAD (Old World Crops Archaeobotanical Database; for excerpts and discussion, see Stevens et al. 2016; Stevens and Fuller 2017), and a relational database expanded from that previously compiled by Lucas (2014) (with references, and building from the previously published and generously shared data and database template of Colledge et al. 2004),[1] with the addition of data compiled in Fuller et al. (2018), and additions from el-Hemmeh (White 2013), Sheikh-e Abad (Whitlam et al. 2018), Gusir Höyük (Kabukcu et al. 2021), Tell Qarassa (Arranz-Otaegui et al. 2016b), Shubayqa 1 (Arranz-Otaegui et al. 2018), Çatalhöyük (Bogaard et al. 2021; for chronological phasing, Hodder 2021), and Jarmo (Gonzalez Carretero et al. 2023). As previously reported (Fuller et al. 2012, 2014, 2018; Maeda et al. 2016; Allaby et al. 2017; Lucas and Fuller 2020) the chronological trends are based on the median calibrated age for sites and phases and as published in Maeda et al. (2016: Table S1); for newer sites the same procedure of summing calibration probability per phase and taking the median of the one-sigma range is used. The previous paper of Fuller et al. (2018) included all sites, regardless of sample size and within assemblage diversity issues, but to improve upon this we have set much higher standards for sample size in the present contribution. Sites included in this study have been reduced to include only phases with assemblages that have more than 10 species and more than 300 individual identified specimens. This eliminates sites that may have had biases due to sampling (e.g. Jericho was not floated), small sample size biases, or contexts that are low diversity due to being storage contexts (e.g. Yiftahl: Garfinkel et al. 1988; Kislev 1985); this removes some of the phases of Çayönü and Cafer Höyük. In the case of Çayönü, the data from Van Zeist and De Roller (1992) is broken into phases following the database of Colledge et al. (2004), while the redating of these phases follows the summary of Hongo (2014) and the supplementary data of Maeda et al. (2016). In the case of Aswad, we have continued to use the data from Van Zeist and Bakker-Heeres (1982) and relevant dating evidence (as per Maeda et al. 2016), and have not incorporated newer datasets. The minimum sample size of 300 is supported by an assessment of richness versus sample size (taxa accumulation curves), both of a selection of individual sites (plotting individual samples) and of the overall site level data (Fig. S2); sample size effects are expected to be much greater below this level. In total we include 95 entries (phase assemblages) in this analysis from 67 sites. The large size of the overall analysis is expected to reduce the impact of sample size effects of individual sites, resulting from differences in sampling (e.g. mesh size), sorting practices and levels of identification. As concluded by previous large dataset analyses, coherent geographical and chronological patterning is evident despite inter-site and inter-laboratory differences in the production of datasets (e.g. Colledge et al. 2004: S46).

The crop presence and percentages considered are based on the potential crop species whether the specimens are assigned to domesticated-type morphology, wild-type morphology, or intermediate status. To account for uncertainty as to what may have been a crop as opposed to gathered, we estimated a higher (maximum crop) percentage and a lower (minimum) estimate. For the first, higher estimate, we considered all cereals, pulses or flax including identifications to genus level and to the species of the wild progenitor, and we included potential grasspea (*Laythrus sativus*), on the potential that these were potential crops in economic terms. This higher estimate is available in the open access dataset of Lucas and Fuller (2018), which we have augmented with more recent datasets for the present analysis. The percentages of the total number of whole specimens for crops were summed for each site/phase considered, following the methodology previously published in Fuller et al. (2018) and Lucas and Fuller (2020), but revised to take a more cautious approach, excluding cereal and pulse indeterminates and specimens identified between two or more genera. For the percentage of crops, we calculated the total number of whole specimens, seeds and chaff, of cereals (*Hordeum spontaneum, H. vulgare, Triticum, and Secale,* excluding indeterminate cereals and specimens identified between two or more genera), pulse taxa (*Pisum, Lens, Lathyrus, Cicer, Vicia ervilia* or *V. faba*) and flax (*Linum* spp. and *Linum usitatissimum*) combined. It will be evident that we have limited our crops/potential crops to the core "founder crops" (see

[1] This dataset is available freely online: Lucas L. and Fuller D.Q., From intermediate economies to agriculture: trends in wild food use, domestication and cultivation among early villages in southwest Asia, 2018 [http://discovery.ucl.ac.uk/id/eprint/10052960].

Zohary 1989; Arranz-Otaegui and Roe 2023), plus *Vicia faba, Lathyrus sativus*, as these are species with known evidence for domestication processes that begin in this region and period, with a long-term legacy as domesticates. We also calculated a lower estimate for crop proportions, excluding genus-level and wild progenitor identifications for *Linum*, *Vicia*, *Pisum*, *Cicer*, and *Lens*. Additionally, all *Lathyrus* species were excluded, and only species-level identifications of *Vicia* as either *V. ervilia* or *V. faba* were included. While other taxa could have been managed or auditioned as cultivars (e.g. Weiss et al. 2006; Melamed et al. 2008; Whitlam et al. 2018; Arranz-Otaegui and Roe 2023), there is a lack of clear morphological evidence that would allow the recognition of which taxa these were, nor that they were widespread across the region with a legacy into later periods; thus such other taxa are assumed to be outside the core founder crop list. These may still include important wild food plants, such as small-grained grasses (Poaceae) (e.g. Savard et al. 2006; Whitlam et al. 2018; Weide et al. 2018) or starchy nutlets of sedges (Cyperaceae) and knotweeds (Polygonaceae), which we regard are likely foods of some importance (Hillman et al. 1989; Savard et al. 2006; Willcox et al. 2009; Asouti and Fuller 2013; Fuller et al. 2018). The key point is that our maximum estimate of percentage crops will tend to over-emphasize the importance of cultivation in our analyses, potentially making Neolithic sites appear more agricultural than they were in reality.

Evidence for the domestication process is drawn from seed size change in assemblages over time and from ratios of shattering to non-shattering rachises. This builds on earlier work (Purugganan and Fuller 2011; Fuller et al. 2012, 2014), which includes estimates of standard deviations around the mean value per sample. For the present purposes we are more interested in overall trends in domestication and rely on the conversion of the mean estimate (of percentage non-shattering or percentage of grain size increase), which allows data across species to be plotted together (a graphing technique introduced in Fuller and Stevens 2017; Fuller et al. 2018; 2023). The estimated mean percentage of non-shattering is based on excluding indeterminates (which have been used in previous analyses to provide error bars and estimates maximum, minimum and standard deviation: Fuller et al. 2012). The seed metric data is from Fuller et al. (2014) and the rachis data, i.e., data on domesticated and wild rachises, is from Allaby et al. (2017), augmented with additional data from Weide et al. (2015), Kabukcu et al. (2021), and Charles et al. (2021); for inclusion of all morphological domestication data we have relaxed our minimum sample size for a few sites only for comparisons between domestication status and crop proportion (e.g. Yarim Tepe, the middle levels of Cafer Höyük).

We also make comparisons between faunal and archaeobotanical data for some sites. We have drawn faunal evidence from a limited number of sources, mainly sub-regional reviews. Archaeobotanical data is drawn from the dataset above. Faunal data considered here is the percentage of sheep and/or goat (*Ovis* and/or *Capra*), regardless of interpreted domestication status, to consider whether there is a general increase in the importance of Caprine herding, or potential herding, alongside crop production. In general, these data considered in terms of percentage of the NISP (number of identifiable specimens, or French NRD), but the methods for calculating percentages may vary to some degree between faunal sources; for example, Martin and Edwards (2013) report this as a percentage of ungulate NISP, whereas other authors report percentage of all mammals. This means that comparability across faunal datasets can only be assured within regional subgroups that come from the same compilation. Nevertheless, trends within regions can be assessed. The data from the southern Levant are from Martin and Edwards (2013); for Anatolia the data are taken from Arbuckle et al. (2014), except for Cafer Höyük, which is from Helmer (2008) and Nevali Çori which is from Peters et al. (2005). Sites from the Northern Levant are taken from Gourichon (2004), and Cypriot data follows Lucas and Fuller (2020).

Supplementary Table S2 lists all the sites considered in the paper (Fig. 4), and indicates which were included in the economic analysis of crop proportion, and those sites included in consideration of morphological domestication (we have relaxed sample size criteria to include a few more sites in this analysis), and those sites considered in terms of proportion of caprine (sheep/goat) faunal remains. Economic data is summarized in Table S3, degrees of morphological domestication in Table S4, caprine data in Table S5, and plant taxa categories including those included in maximum and minimum estimates of crops, in Table S6.

Results and discussion

The archaeobotanical data strongly indicate a great degree of intermediacy in levels of reliance on cultivars versus wild foods. Maeda et al. (2016) already showed the widespread trend that proportions of cereals increase, especially throughout the PPNB, but also there is a great degree of variability in the proportion of cereals (explored also in relation to the uses of various wild foods by several authors, e.g. Arranz-Otaegui et al. 2016a; Weide et al. 2018). As already noted in Fuller et al. (2018) sites in which foraging appear dominant were more common before 8500 BC than later, and there are very few sites before 8500 BC with unambiguously agricultural economies (assemblages dominated by potential crop plants, including in their wild forms). We can look at this on a timeline by plotting the simple percentage of crops among all plant remains for each

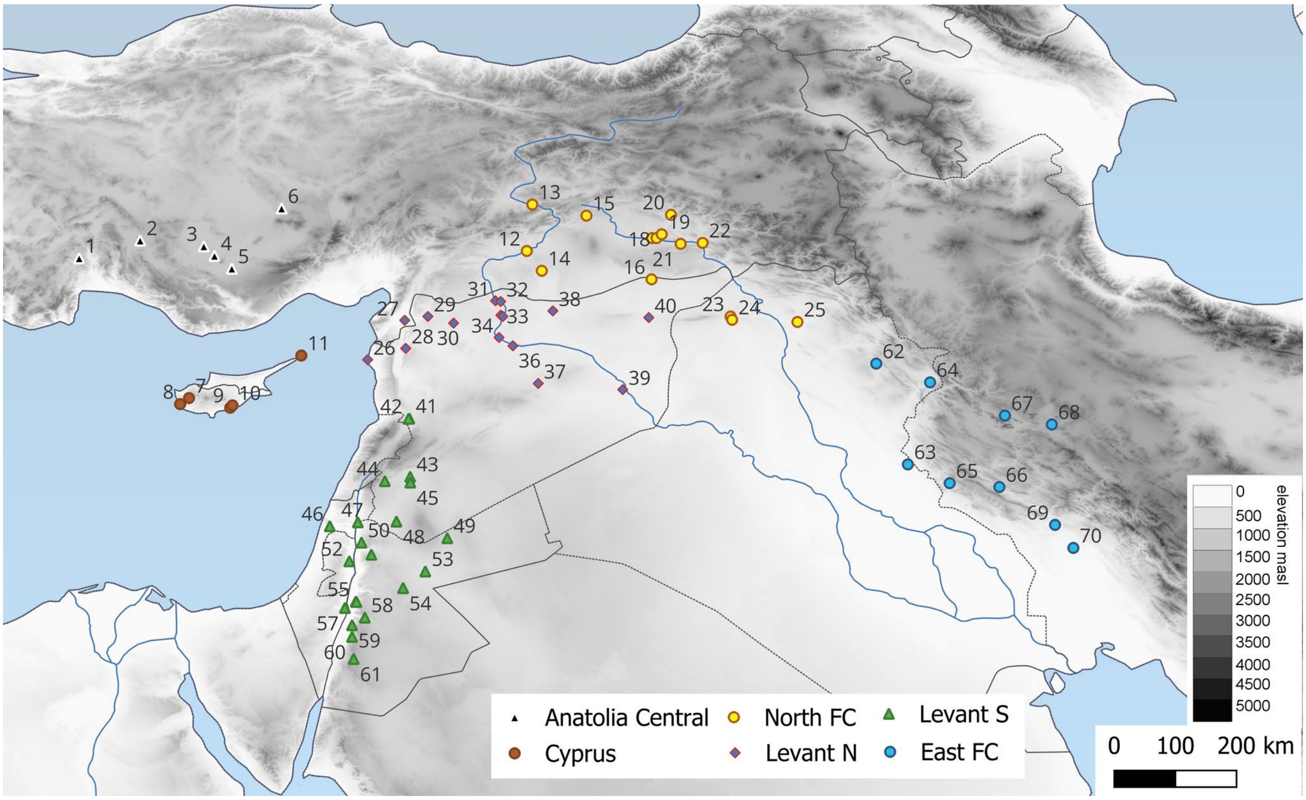

Fig. 4 Map of Epipalaeolithic and Neolithic sites discussed in this article, divided into regional groupings. Anatolia Central: 1. Höyücek, 2. Erbaba, 3. Çatalhöyük, 4. Pınarbaşı, 5. Can Hassan III, 6. Aşikli Höyük, 7. Krittou Marottou 'Ais Yiorkis, 8. Kissonerga Mylouthkia, 9. Kalavasos Tenta, 10. Khirokitia, 11. Cape Andreas-Kastros; 12. Nevali Çori; 13. Cafer Höyük, 14. Göbekli Tepe, 15. Çayönü, 16. Tell Aqab, 17. Salat Cami Yani, 18. Körtik Tepe, 19. Demirköy, 20. Hallan Çemi Tepesi, 21. Hasankeyf Höyük, 22. Gusir Höyük, 23. Mazgaliyeh, 24. Yarim Tepe, 25. M'lefaat, 26. Tell Ras Shamra, 27. Tell Kurdu, 28. Tell El-Kerkh, 29. Dederiyeh Cave, 30. Tell Qaramel, 31. Tell 'Abr, 32. Dja'de, 33. Tell Hallula, 34. Tell Mureybit, 35. Jerf al Ahmar, 36. Tell Abu Hureyra, 37. El Kowm, 38. Tell Sabi Abyad, 39. Tell Bouqras, 40. Umm Qseir, 41. Arjoune, 42. Tell Nebi Mend, 43. Tell Ghoraifé, 44. Tell Ramad, 45. Tell Aswad, 46. Nahal Zehora, 47. Sha'ar Hagolan, 48. Tell Qarassa, 49. Shubayqa, 50. Iraq ed-Dubb, 51. Jebel Abu Thawwb (er-Rumman), 52. Netiv Hagdud, 53. Azraq 31, 54. Wadi Jilat 7 & Wadi Jilat 13, 55. Zahrat Adh-Dhra (ZAD) 2, 56. Dhra', 57. Nahal Hemar, 58. El-Hemmeh, 59. Wadi Fidan A 60. Wadi Fidan C, 61. Basta, 62. Jarmo, 63. Choga Mami, 64. Tepe Marani, 64. Choga Golan, 66. East Chia Sabz, 67. Sheikh-e Abad, 68. Ganj Dareh, 69. Ali Kosh, 70. Chogha Bonut. Coordinates in Table S2

individual site assemblage (Fig. 5), as well as looking at each period in terms of the proportions of sites with varying levels of crops (Fig. 6). These data indicate that in the Epipalaeolithic we have clearly wild-focused economies (~1%—4.82%, maximum; ~1%—1.37%, minimum), with only Tell Qaramel having what registers as a mixed-subsistence economy with ~32.77% (maximum). However, if the minimum crop percentage is used, Tell Qaramel is at the higher range of foraging-focused with 22.41% (minimum) crop remains. Of note, the sampled levels at this site span the late Epipalaeolithic and PPNA to as late as ca. 9000 BC (Mazurowski et al. 2009). Thus, the reported archaeobotany, which is undifferentiated through these phases, can be considered alongside that of Early Jerf el Ahmar and PPNA Tell Mureybet as representing a mixed-subsistence economy with significant wild crop or progenitor use, either gathered or under incipient pre-domestication cultivation (see also Willcox et al. 2009). During the subphases of the Pre-Pottery Neolithic B we find a mix of economic systems, with mixed-subsistence systems dominating and small minorities of agriculturally-dominated assemblages, as well as foraging-focused systems. At the other end of the timeline, during the ceramic Neolithic periods, a majority of sites, regardless of sub-region, show close to 50% crops (maximum), and 42% of sites have more than 75% crops. This indicates an increase in crop-dominated economies at this time. Only a few sites represent foraging-focused economies (Table 4), such as Choga Mami (14.33% maximum; 13.6% minimum crops) and Ali Kosh (~20% Ali Kosh phase, 2.2% Mohammad Jaffar phase). Both sites are in the distant eastern wing of the Fertile Crescent. This suggests a persistence in high levels of wild food (especially wild grass) use in the region, where a similarly low level of crop use was already evident in the earlier site of Choga Golan before 8000 BC (see Fuller

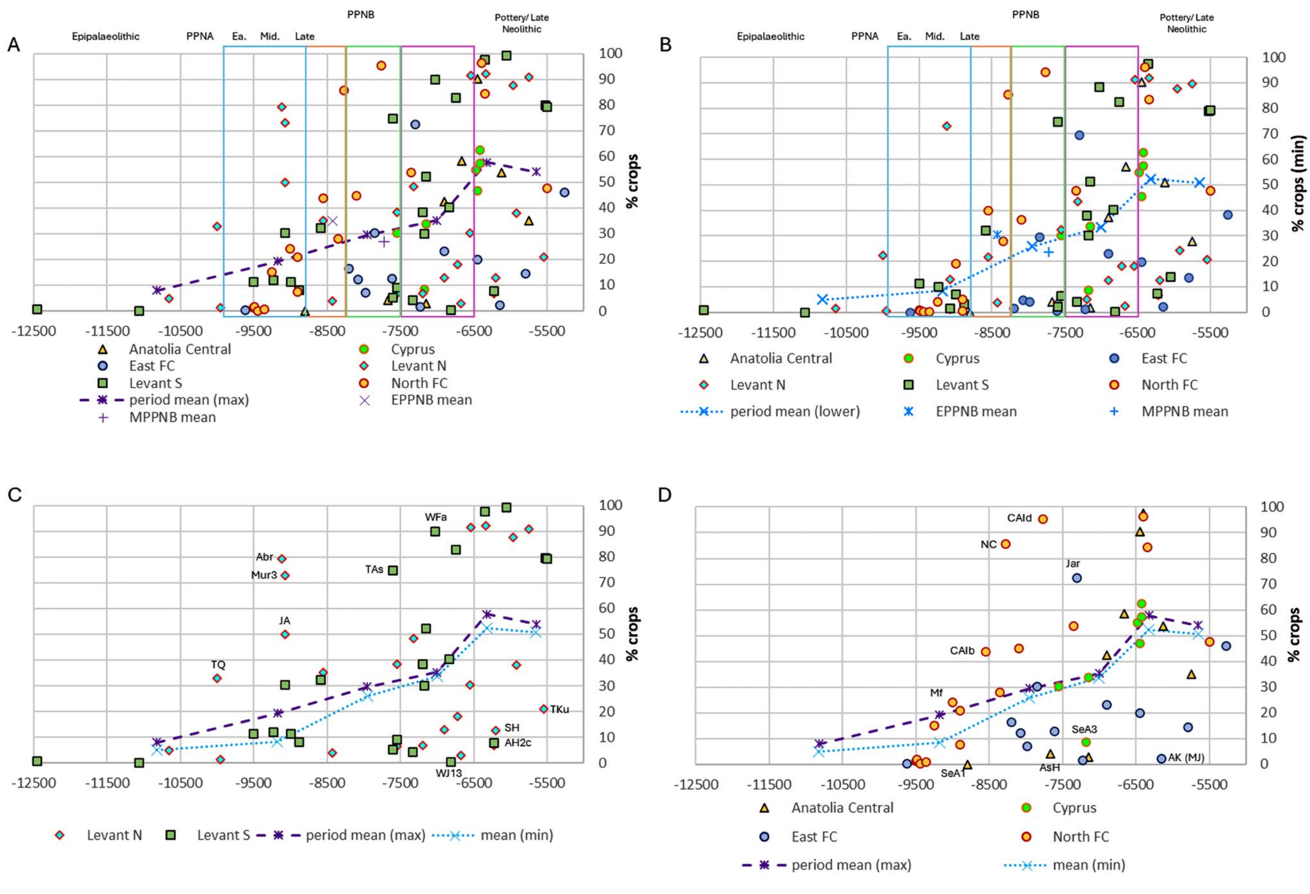

Fig. 5 Charting the rising importance of crops, the occurrence of mixed-subsistence economies, and the decline in wild food use. **A** Plots the percentage of crops (maximum estimate) out of all plant remains against the median age of each site. The averages of the broader period cohorts are shown with trendlines (EPPNB and MPPNB combined). **B** Plots the lower crop estimate with trendlines and period averages adjusted accordingly. **C** Plots sites from the North and South Levant only (maximum crop estimate) with selected outlier sites labelled, with upper and lower average trend lines indicated. **D** Plots sites from Central Anatolia, Cyprus, the North and East Fertile Crescent regions (maximum crop estimate) with selected outlier sites labelled, with upper and lower average trend lines indicated. Data: Table S3. Labelled site codes: TQ = Tell Qaramel, JA = Jerf Al Ahmar, Mur3 = Mureybit III, Abr = Tell ʻAbr, TAs = Tell Aswad, WFa = Wadi Fidan A, WJ13 = Wadi Jilat 13, SH = Sha'ar Hagolan, AH2c = Abu Hureyra 2C, TKu = Tell Kurdu; SeA1 & SeA3 = Sheikh-e Abad 1, 3, Mf = M'lefaat, CA1b & CA1d = Çayönü phases, NC = Nevalı Çori, Jar = Jarmo, AsH = Aşıklı Höyük, AK (MJ) = Ali Kosh Mohamed Jaffer phase

et al. 2018, Table 1; Riehl et al. 2013), and where extensive wild grass exploitation has been indicated in the archaeobotanical evidence, as explored by Weide et al. (2017, 2018) and Whitlam et al. (2018).

In the PPNA, we observe a predominance of foraging-focused economies (77.78% maximum; 94.44% minimum), with 16.66% (maximum) classified as mixed-subsistence. One site, Tell ʻAbr, located in the Northern Levant, has more than 75% crops in its assemblage (79.28% maximum; 72.95% minimum) (Fig. 6, Table 1). However, the data is thought to derive mainly from burned stores that are biased towards cereals, in particular wild rye, *Secale montanum/vavilovi* (Willcox et al. 2008; Douche and Willcox 2023). Despite a robust sample size (3531 seeds, 10 taxa), the sampling bias at this site may mask the diversity of wild resources, although it remains important evidence for the likely pre-domestication cultivation of a regional lost rye crop. Regional contrasts appear with more reliance on crops, above the period average, found on sites from the Northern Levant (e.g., Tell Qaramel, Jerf el Ahmar, Tell Mureybet) and southern Levant (e.g., Dhra', Netiv Hagdud, El-Hemmeh). Sites in the northern Fertile Crescent tend to have fewer potential crop remains and fall into the foraging-focused category. Instead Northern Fertile Crescent sites tend to suggest a strong focus on nuts (e.g. Hasankey Höyük, Gusir Höyük) or starchy nutlets (e.g. Demirköy, Hallan Çemi). The site of M'lefaat could be an outlier in this region with a possibly high estimate of potential crops, if the large legume fragments of *Vicia/Lathyrus* type are included. However, we have not included them as crops in this analysis, which returns a maximum crop percentage of 24% and a minimum around 19%, divided between

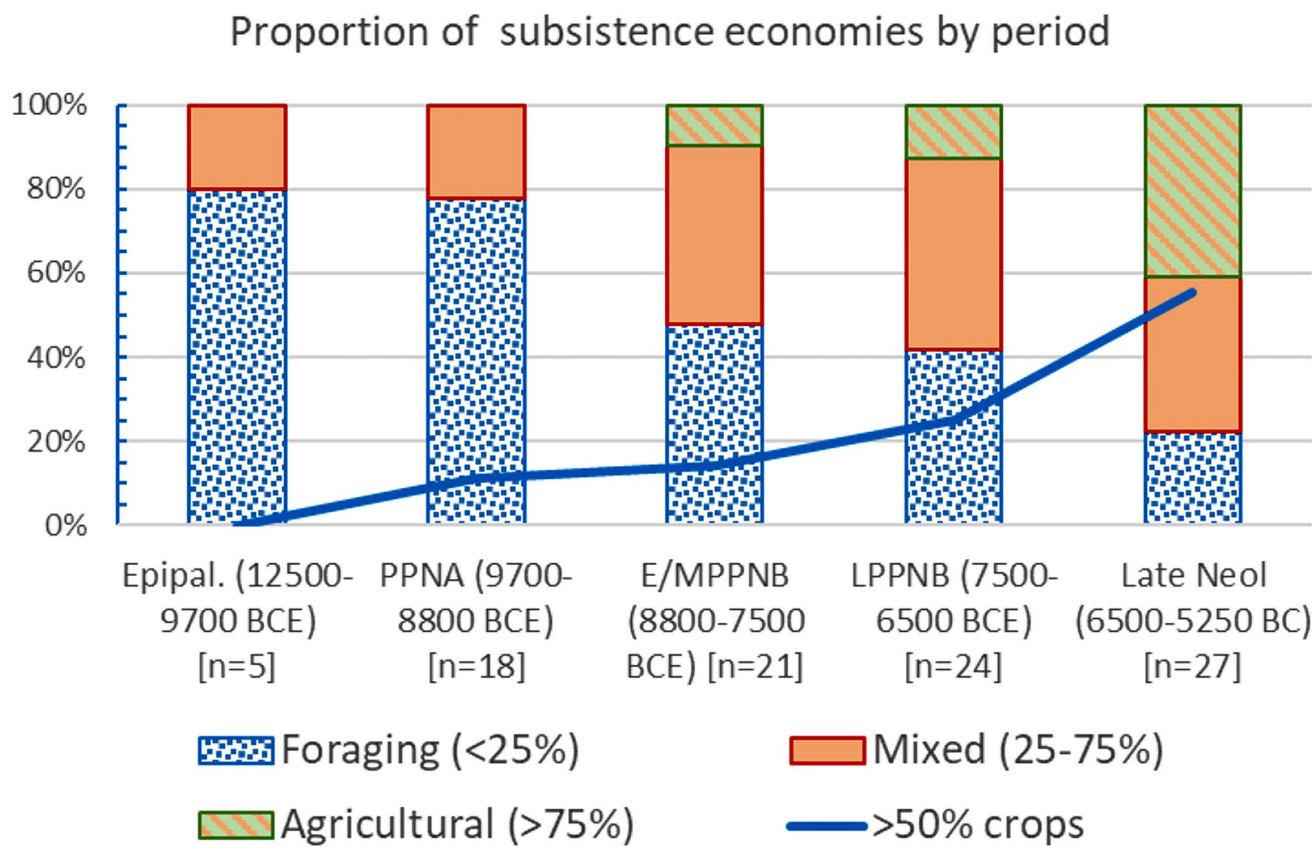

Fig. 6 Graph of the proportion of sites in each archaeological phase that are classed in each economic group, as well as indicating the proportion that would be regarded as "Low-Level Food Production" (i.e., less than 50% crop remains) below the blue line. Included sites all have a minimum of 10 taxa and 300 items. Number of sites in each phase indicated. Data: Table S3

lentils and cereals (both *Hordeum* and *Triticum*). This is the only site in the region with a potential case to be argued for cultivation as the assemblage also includes a number of "obligate" and facultative weeds (sensu Willcox 2012; Fuller and Stevens 2019), including *Adonis, Bellevalia, Coronilla, Heliotropium, Lolium rigidum/perenne, Vaccaria* (Savard et al. 2006). Other authors noting such regional differences between the Levant and Northern Fertile Crescent have argued for the extension of cereal cultivation northwards from the Levant in the Early PPNB (e.g. Arranz-Otaegui et al. 2016a), which also fits with recent evidence at Gusir Höyük where EPPNB levels show the arrival of einkorn and emmer wheat (Kabukcu et al. 2021). Nevertheless, temporal trends in each region tend to recapitulate the trans-regional process of increasing proportions of crops occurring on sites over time; such a trend is especially evident in the Northern Fertile Crescent sites moving into the EPPNB onwards, whereas in the northern and southern Levant there are some sites in all periods of the Pre-Pottery Neolithic that fall in the foraging-focused category. This suggests that some communities may have continued to focus on foraging, even while others put efforts into cultivation.

While the PPNA is when pre-domestication cultivation is widely inferred (e.g., Willcox 2012; Asouti and Fuller 2013; Arranz-Otaegui et al. 2016a; Colledge et al. 2018; Fuller and Stevens 2019), there is nothing that can be regarded as agricultural with a heavy reliance on early crops (if we exclude Tell 'Abr, as discussed above). Recent consideration of early "arable weeds" from the PPNA has called into question routine, systematic cultivation in contrast to later pre-pottery (EPPNB and MPPNB) sites (Weide et al. 2021; 2022), although this remains disputed (Willcox 2023; 2024; Stevens and Fuller 2024). Instead, the weed flora is more consistent with that of disturbance within native grassland habitats rather than replacement with cleared fields of monoculture. Where increases in grain size are evident (e.g. Jerf el Ahmar, EPPNB Dja'de, EPPNB Çayönü), it is likely that much more routine cultivation was necessary to set a selection process in motion, in which seedling competition in cleared, sown fields favoured seed volumes, increases (as per Fuller et al. 2010; 2023; Allaby et al. 2022a; 2022b). Grain size increases are evident by the end of the PPNA (Willcox 2004; Fuller et al. 2014; and see below). Asouti and Fuller (2013: 328) suggested management would have included

Table 1 The classification of economic commitment to cultivars in assemblages with median ages from 10,600 to 8800 BCE (terminal Epipalaeolithic to PPNA horizon)

Pure foraging (0–1% crop taxa)	Foraging-focused (1–25% crop taxa)	Mixed subsistence (25%–75% crop taxa)
Hasankeyf Höyük Ve Vf Lc Ps	Tell Abu Hureyra 1 T2g Sc Lc Ve	Tell Qaramel Hv Tm Td Lc Ve
Demirköy Hv Td Lc	Tell Mureybit II Hv Td T2g Sc Lc Ps Lu	Netiv Hagdud Hv Td Lc Ve
Shubaqya Hv Tm	Dhra' Hv T	Tell Mureybit III Hv T2g Sc Lc Ps Ve
Pınarbaşı Tm	El-Hemmeh Hv Td Le Ve	Jerf el Ahmar Hv Tb T2g Sc Ps Ve
Sheikh-eAbad 1 T Hv Lc Ps Ve	Zahrat Adh-Dhra (ZAD-2) Hv T. Le	
	Gusir Hoyuk 1 Lc Ve	
	Gusir Hoyuk 2 Tb Td Lc Ve	**Crop-dominated** (> 75% crop taxa*)
	Körtik Tepe Hv Sc Tm Le	Tell ‘Abr Hv Sc Tm Le *biased, storage contexts only
	Iraq ed Dubb Hv T	
	Göbekli Tepe Hv Tm	
	M'lefaat II Hv T. Le	
	Hallan Çemi Tepesi II Hv T. Lc Ps Ve	

The percentages are based on the maximum percentage. Cultivars or wild progenitors presence indicated: Hv = *Hordeum vulgare* sensu lato*;* Td = *Triticum dicoccum/dicoccoides;* Tm = *Triticum monococcum/boeoticum;* T2g = two-grained einkorn*;* T. = *Triticum* sp. [only where more specific identifications are not available]; Tda = *Triticum turgidum/aestivum* (free-threshing); Sc = *Secale* sp.*;* Ca = *Cicer arietinum;* Lc = *Lens* sp./*culinaris*; Ps = *Pisum* sp./*sativum;* Ve = *Vicia ervilia;* Vf = *Vicia faba;* Lu = *Linum usitatissimum*

“harvesting and replanting of cereal stands at sites located within the natural distribution zones of the wild progenitors (e.g., Tell el-Kerkh, Tell Qaramel), and outside these zones the opportunistic sowing of select cereal species at dispersed localities in the landscape (e.g., Mureybit, Jerf el Ahmar, Tell ‘Abr 3, Dja’de).” While the above examples were all drawn from the Northern Levant, the rise in crop taxa frequencies illustrated in Fig. 5, suggests a similar mix of practices in parts of the Southern Levant but perhaps not in the Northern Fertile Crescent, Central Anatolia or the Eastern Fertile Crescent. These practices of early management and cultivation supported some growth in population density within communities: during the Epipalaeolithic site size data indicates sizes generally less than 0.3 ha (Guerrero et al. 2008), whereas many PPNA sites with cultivation are in the ~ 0.5 ha (e.g. Netiv Hagdud, Mureybit), 1 ha (Jerf el Ahmar), and up to 3 ha size range (e.g. Qaramel) (Van Loon 1968; Mazurowski 1999; Guerrero et al. 2008; McBride 2015), suggesting the returns of more intensive land use, and the increased yields of larger average grain sizes (Fuller et al. 2010), would support more, and more sedentary, populations.

During the PPNA to the Early PPNB we can think of weeds becoming defined in contradistinction to early crops. As noted over 40 years ago by Reed (1977, 901), “the concept of the weed may have been born as the more successful natural vegetation was pulled and hacked out, the ground pried at with digging sticks, and seeds [of crops] scattered and covered.” When cultivation became more routine and intensive, some of these non-crops persisted as better adapted to cultivation, and thus became true arable weeds. As noted in Fuller and Stevens (2019) it is only from the Early PPNB that there is a strong correlation between levels of cereal use and increasing presence of a greater range of arable weeds: this suggests that human land use practices, and harvesting and processing of plant foods increased the regularity with which the emergent weed flora came into settlement contexts alongside crops. Archaeobotanical data highlights the high weed diversity associated with early cultivation in the Levant (Colledge et al. 2004), and it remains to be understood whether there was something about practices and ecologies in the Levant in particular that engendered the origins of a major component of the arable weed flora in distinction to other regions, and how this may correlate with selection for domestication traits in cereals or pulses.

Equally some communities and regions focused on wild foods, and likely practised little or no substantive cultivation. This is the case in the Northern Fertile Crescent, represented by sites such as Hasankeyf Höyük, Hallan Çemi and Demirköy, all of which have been characterized as sedentary hunter-gatherer sites that characterized the Upper Tigris area during the PPNA period (see Savard et al. 2006; Maeda 2018). Here communities may have developed sedentism around hunter-gatherer-fisher systems in the rich opportunities provided by the many rivers flowing out of the well-watered eastern Taurus mountains. Wild progenitors were native to the hilly flanks here and exploited, from wild pig (Zeder and Lemoine 2022) and wild sheep (Itahshi et al. 2017), to wild lentil and bitter vetch (Kabukcu et al. 2021). Although dubbed as a "steppe Mesolithic" (Graeber and Wengrow 2021), these traditions were focused on resources of woodland (nuts), woodland margin (wild legumes) and often wetlands (Cyperaceae and Polygonaceae nutlets, fish). As noted above, M'lefaat is a possible outlier in such a regional scenario and a plausible "false start" of a cultivation/domestication trajectory, but it could also represent steppe gathering that included wild cereals and incidental collection of the progenitors of later weed taxa.

During the Early and Middle PPNB, mixed-subsistence economies predominate, with the first occurrence of a few sites leaning towards crop-dominance, or something more agriculturally focused (Table 2). When combined, these periods have about half of their assemblages classified as foraging-focused (47.62% maximum; 52.38% minimum), 42.85% (maximum) as mixed-subsistence, and less than 10% (9.52% maximum and minimum) as crop-dominated. The shorter and less well sampled Early PPNB (8700–8200 BC) is represented mainly in the northern Levant, where the foraging-focused Tell El Kerkh 2 (3.9%) that still produced a diverse range of likely cultivars including cereals and pulses showing evidence for morphological change of domestication (see Tanno and Willcox 2006b; 2012). One outlier with very low-levels of crops is Asikli Höyük (4.05%) (based on Van Zeist and De Roller 1995), but this is accounted for by very high numbers of mineralized *Celtis* seeds; excluding these raises the crops to ~21%, still in the

Table 2 The classification of economic commitment to cultivars in assemblages with median ages from 8800–7500 BCE (Early and Middle PPNB horizon)

Foraging-focused (1–25% crop taxa)	Mixed subsistence (25%–75% crop taxa)	Crop-dominated (75%–100% crop taxa)
Tell El-Kerkh 2 EPPNB **Hv Td Tm T2g Ca** Lc Ve **Vf**	Tell Qarassa EPPNB **Hv Tm Td** Lc Ve Vf Ps	Nevali Çori EPPNB Hv Td **Tm T2g** Lc **Ps** Ve **Vf**
Aşıklı Höyük MPPNB **Hv Tb Td Tt Lc** Ps Ve	Dja'de EPPNB **Hv** Td Tm **T2g** Sc Lc Ve Vf Ps	Çayönü Id MPPNB Hv **Td Tm** Ca Lc **Ps** Ve **Vf** Lu
Nahal Hemar MPPNB **Hv** Td Lc Ls Lu	Gusir Hoyuk 3 EPPNB **Tm Td** Lc Ve	
Tell El-Kerkh 3 MPPNB **Hv Td Tm T2g Ca** Lc Ve **Vf**	Cafer Hoyuk (XIII-IX) MPPNB Hv **Tm Td** Tt Sc Lc Ps Ve **Vf**	
Tell Abu Hureyra 2A MPPNB **Hv Tm** Sc Lc Lu	Krittou Marottou 'Ais Yiorkis MPPNB **Hv T2g** Lc Ps Ve	
Sheikh-eAbad 2 MPPNB **Hv** T Lc Ps Ve	Tell Hallula MPPNB **Hv Td** T2g **Lc** Ps Ve **Vf** Lu	
Sheikh-eAbad 3 MPPNB **Hv** Le Ve	Tell Aswad MPPNB* **Hv Td** Tm **Tda Lc** Ps Ve Lu * borderline ~ 75%	
Wadi Jilat 7 MPPNB Hv **Td Tm T2g** Lc Ve	Ganj Dareh **Hv Le** Ps	
Chia Sabz MPPNB Hv T Le	Çayönü Ib EPPNB Hv **Td Tm** Ca Lc **Ps** Ve **Vf** Lu	
Chogha Golan EPPNB T Hv		

The percentages are based on the maximum percentage. Cultivars or wild progenitors with presence is indicated: Hv = *Hordeum vulgare* sensu lato*;* Td = *Triticum dicoccum/dicoccoides;* Tm = *Triticum monococcum/baeoticum;* T2g = two-grained einkorn*;* T. = *Triticum* sp. [only where more specific identifications are not available]; Tt = *Triticum timopheevi;* Tda = *Triticum turgidum/aestivum* (free-threshing); Sc = *Secale* sp.*;* Ca = *Cicer arietinum;* Lc = *Lens* sp./*culinaris*; Ls = *Lathyrus* sp./sativus; Ps = *Pisum* sp./*sativum;* Ve = *Vicia ervilia;* Vf = *Vica faba;* Lu = *Linum usitatissimum.* Crops with evidence for morphological change (semi-domesticates or domesticates) indicated in bold (based on morphological change data compiled in Fuller et al. 2012; 2014; 2018; Allaby et al. 2017) foraging-focused category. More recent sampling on a larger scale, has returned just under 25% crops for the lowest levels (equivalent to latest EPPNB through earlier part of the MPPNB: Stiner et al. 2021), but shows an increasing proportion of crops to ca. 50% in later levels (Ergun 2018). Apparently crop-dominated outliers in the Northern Fertile Crescent include Nevali Çori. Nevali Çori remains may be biased by sampling that included hearths with large concentration of cereal chaff, but even ignoring the ~ 26,000 chaff remains there were many hundreds of cereal grains and pulse seeds, and more modest amounts of wild seeds and nutshell (Pasternak 1998); these finds have not been directly dated but are reported from the PPNB levels rather than overlying Bronze Age deposits. The predominantly wild status of both barley (Pasternak 1998) and einkorn wheat chaff (Tanno and Willcox 2006a; 2012), fits best with an early PPNB date, but the 11–32% domesticated einkorn chaff (amongst determinable remains: Tanno and Willcox 2012) indicates this was under cultivation. Excluding all chaff remains, crop seeds account for ~ 40% (maximum) of all seed remains (a lower estimate 37.25%, excluding *Lathyrus sativus* and "unidentified pulses"), which would still place this site as above average for its period, but as a mixed economy. Its pulse remains, including *Vicia faba* and larger sized *Pisum* could suggest domestication processes (Pasternak 1998), but further metrical studies and dating would be helpful. All of the above as well as plausible obligate arable weeds point to cultivation and ongoing domestication processes (see previous discussions in Nesbitt 2004; Willcox 2007; Fuller et al. 2012; Asouti and Fuller 2013). Thus, while reanalysis and dating are warranted, this site also suggests an important role for cultivation and culti-wilds. At the end of the Middle PPNB, Çayönü 1D (Cell building), shows high crop remains (95.4% maximum) which is partly accounted for a nearly pure sample of more than 3600 bitter vetch seeds from inside one house (Van Zeist and De Roller 1992: 92), but even excluding this, returns 68.3% crops (maximum estimate) or 60.4% (lower estimate), which is still above average for its age. Tell Aswad is also high, nearly 75% (maximum and minimum), and is an extensively sampled site (Van Zeist and Bakker-Heeres 1982), even without incorporating the new samples and subphases that also provide a rich and diverse crop assemblage with semi-domesticated cereal assemblages (Douche and Willcox 2018).

On the whole, these periods of the Early and Middle PPNB highlight the concurrent existence of foraging-focused and crop-dominated assemblages, as well as a large number of mixed-subsistence economies. For the most part crops appear closer to morphologically wild, with some semi-domesticated forms indicated by larger-than-average sizes (cereals at Dja'de, einkorn and pea at Çayönü) and appearance, but not dominance of non-shattering rachises (e.g. Nevali Çori, Cafer Höyük, Tell Qarassa) (see Tanno and Willcox 2012; Fuller et al. 2012; 2014; Arranz-Otaegui et al. 2016a). The Middle PPNB is likely to correspond to the PPNB phase at Jericho with its reported domesticated cereals (Hopf 1983; Asouti and Fuller 2012). This is also the period when mixed subsistence and some domesticated morphotypes appear widely in the Northern Fertile Crescent and Eastern Fertile Crescent. Fundamental changes took place in the Pre-Pottery Neolithic B as pre-domestication cultivation was intensified by some communities and became entrenched through the increased frequency of domestication genes implied by morphological change. Changes included individual household storage, and by inference more household investment in land (Bogaard et al. 2009; Asouti and Fuller 2012; 2013; Weide 2021; Weide et al. 2022).

The LPPNB sees a slight decline in foraging-focused site assemblages alongside the continuance of mixed-subsistence economies (Table 3). The use of 50% food plants as a dividing line, suggested by the Low-level Food Production framework (LLFP), makes for little difference from the PPNA to the Late PPNB, suggesting that LLFP framework is less informative when it comes to contrasting the economies across the Pre-Pottery Neolithic, than use of the mixed-subsistence rubric (Fig. 6). By around 7550 BC, 'Ais Yorkis on Cyprus previously appeared to be crop-dominated (Lucas and Fuller 2020; Fuller et al. 2018). However, when considered alongside the more conservative methodological approach (i.e.excluding cereal indeterminates) used here and the context from which the majority of grains were recovered (a single pit)(Lucas et al. 2012), this raises the issue of a sample biased towards a storage-related context that underrepresents wild resources. Consequently, 'Ais Yorkis is likely to represent mixed-subsistence, with crops accounting for 30% (both maximum and minimum). Other sites on the island from the LPPNB (Table 3) are mixed-subsistence or foraging-focused. This period tends to produce evidence for fully domesticated crops in terms of non-shattering (Allaby et al. 2017), although grain size increase is still under way (Fuller et al. 2014; 2017). 'Ais Yorkis on Cyprus suggests a more precocious or accelerated evolution of larger-grained cereals on the island (Lucas et al. 2012), even if economies were largely mixed. The animal economy on Cyprus in this period included some herded animals but also the intensive hunting of wild/feral animals that had been introduced to the island, including deer but also pigs and feral caprines (Croft 1991; 2002; Lucas and Fuller 2020). The increased productivity of domesticated or near-domesticated crops and higher levels of reliance on crops in the LPPNB period correlates with a period that sees increased site sizes, including "mega-sites" of 9 to 12 ha in the southern Levant, 13 ha at Abu Hureyra 2B/C and Çatalhöyük (Kuijt 2000; Moore et al. 2000; Verhoeven 2006; Der and Isaavi 2017), that imply the economic base (more agricultural) for supporting higher population densities was in place.

Table 3 The classification of economic commitment to cultivars in assemblages with median ages from 7500–6500 BCE (Late PPNB horizon)

Foraging-focused (1–25% crop taxa)	Mixed subsistence (25%–75% crop taxa)	Agriculture (75%–100% crop taxa)
Tell Abu Hureyra 2B **Hv Sc Td T2g Tda Lc Ps** Ve **Vf** Lu	Tell Nebi Mend **Hv Td Tm Lc**	Tell Ramad II **Hv Td Tm** T2g **Ca Le Ps** Ve Lu
El Kowm II **Hv Td Tm T2g** Ve	Jarmo **Hv Td Tda Tt Lc** Ps Ve Lu	Tell Ras Shamra Vb **Hv Td Lc Ps** Lu
Can Hasan III **Hv Sc Td Tm Tda Lc Ps** Ve	Tell Hallula (HEP) **Hv Td** T2g **Tda** Ps **Vf** Lu	Wadi Fidan A **Td Hv Tm**
Tell Bouqras **Hv Td Tm Tda Lc Ps** Lu	Tell Hallula (LB) **Hv Td Tda Lc** Ps Lu	
Wadi Jilat 13 **Hv Td Tm**	Tell Ramad I **Hv Td Tm** T2g **Ca Le Ps** Ve Lu	
Ali Kosh (Bus Mordeh) **Hv Td Tm** Lu	Kissonerga Mylouthkia 1B **Hv Td Tm** Le Lu	
Azraq 31 **Tda Hv**	Tell Ghoraife **Hv Td Tm Tda Lc Ps** Ve Lu	
El Kowm 1A **Td TdaHv Ps**	Cafer Höyük (IV-I) **Hv Td Tm** Tt **Tda** Sc Le Ls	
Chogha Bonut **Td Tm Lc**	Çatalhöyük Early **Hv Td Tm Tt Tda Ca Lc Ps** Ve	
Kalavasos Tenta **Hv Tm** Le	Çatalhöyük Middle **Hv Td Tm Tt Tda Ca Lc Ps** Ve La	

The percentages are based on the maximum percentage. Cultivars or wild progenitors presence indicated: Hv = *Hordeum vulgare* sensu lato*;* Td = *Triticum dicoccum/dicoccoides;* Tm = *Triticum monococcum/baeoticum;* T2g = two-grained einkorn*;* T. = *Triticum* sp. [only where more specific identifications are not available]; Tt = *Triticum timopheevi;* Tda = *Triticum turgidum/aestivum* (free-threshing); Sc = *Secale* sp.*;* Ca = *Cicer arietinum;* Lc = *Lens* sp./*culinaris*; Ls = *Lathyrus* sp./sativus; Ps = *Pisum* sp./*sativum;* Ve = *Vicia ervilia;* Vf = *Vica faba;* Lu = *Linum usitatissimum.* Crops with evidence for morphological change (semi-domesticates or domesticates) indicated in bold (based on morphological change data compiled in Fuller et al. 2012, 2014, 2018; Asouti and Fuller 2013; or Allaby et al. 2017)

After 6500 BC, during the latest Pre-Pottery Neolithic levels in some areas (such as the southern Levant) and the early ceramic period in most other areas, agricultural economies increased from 12% (maximum) to 42.30% (maximum) (Table 4). The site of Höyücek is represented by burnt stores of a range of weed-infested crops (Martinoli and Nesbitt 2003), and thus likely under-represents wild foods and other seeds. Although Martinoli and Nesbitt (2003) initially suggested this could be stores dominated by wild-type einkorn as it includes some shattering rachises, grain metrics favour a domesticated form (Fuller et al. 2012), indicating that this must have been under cultivation and selection still, which is notable for the later, pottery period date of this site. Crop-dominated sites, however, are still not universal but mixed-subsistence systems are evident at various sites throughout the Fertile Crescent, Anatolia and Cyprus. A small number of sites have more foraging-focused assemblages. For example, El Kowm, which has fewer crops in this period than earlier phases, which raises the question as to whether there is some retreat from cultivation during this period, which is sometimes seen as a period of decline in population density (e.g. Simmons 2000; Kuijt 2000; Özdoğun 2024). In addition, foraging-focused systems persisted on the desert margins of the Southern Levant, represented by Wadi Jilat 13 (Colledge 2001). It is notable that this region has also produced similarly late assemblages dominated by wild barley rachis that suggest parts of the semi-desert regions of Jordan lay outside the areas in which barley was undergoing domestication (Colledge 2001; Fuller 2007; Fuller et al. 2018; see below). Nevertheless, this is the period associated with most rapid geographical expansion of Neolithic societies with a package of domesticated plants and animals both eastwards and westwards from the greater Fertile Crescent (e.g. Lepperd 2022; Özdoğun 2024).

Comparing domestication and agriculturalization processes

To look in further detail at the relationship between domestication processes and economic change we compare domestication traits with proportion of crops for the subset of sites that have data for both (Fig. 7). Non-shattering data, when available, is based on the proportions of emmer, einkorn or barley rachis remains with scars while grain size increase is calculated as the percentage increase of the assemblage mean in grain thickness of wheat (emmer or einkorn) and grain width of barley (these are the dimensions that show the most marked change during domestication). Such data have mostly

Table 4 The classification of economic commitment to cultivars in assemblages with median ages from 6500–5000 BCE (Pottery Neolithic horizon)

Foraging-focused (1–25% crop taxa)	Mixed subsistence (25%−75% crop taxa)	Agriculture (75%−100% crop taxa)
Tell Abu Hureyra 2C **Hv Sc Td Tm Tda** Lc Lu	Cape Andreas Kastros **Hv Td Tm Lc Ps** Vf Lu	Nahal Zehora **Hv Td Tda**
Sha'ar Hagolan **Hv Td Tm Tda** Lc Lu	Çatalhöyük (Late) **Hv Td Tm Tt Tda Lc Ps**	Umm Qseir **Hv Td Ca Lc** Ve
El Kowm 1B **Hv Td Tda** Lc	Çatalhöyük West **Hv Td Tm Tt Tda Ca Lc Ps** La	Erbaba **Hv Td Tm Tda Lc Ps** Ve
Ali Kosh (M.Jaffar) **Hv Td** Lc Lu	Tell Hallula **Hv Td Tm Tda** Lc Ps **Vf Lu**	Çayönü II **Hv Td Tm Le** Ve
Ali Kosh (Ali Kosh) **Hv Td Tm** Lc Lu	Tepe Marani **Hv Td Tm Tda Ca Lc Ps** Ve **Vf**	Wadi Fidan C **Hv Tm Le**
Choga Mami **Hv Td Tm Tda** Lc Ps Lu	Tell Aqab **Hv Td Lc** Ve **Lu**	Salat Cami Yani **Hv T.** Lc Ps Lu
Tell Kurdu **Hv Tm Ca** Lc Ps Lu	Khirokitia 4 **Hv Td Tm** Lc	Tell Ras Shamra Va **Hv Td Tm Lc Ps** Lu
	Khirokitia 3a/3b **Hv Td Tm** Lc	Arjoune **Hv Td Tm Tda Lc Vf**
		Tell Sabi Abyad **Hv Td Tm Lc** Lu
		Höyücek **Td Tm Tda Ca** La **Le** Ve
		Jebel Abu Thawwb **Hv Td Tda Lc** Ps

The percentages are based on the maximum percentage. Cultivars or wild progenitors presence indicated: Hv = *Hordeum vulgare* sensu lato*;* Td = *Triticum dicoccum/dicoccoides;* Tm = *Triticum monococcum/baeoticum;* T2g = two-grained einkorn*;* T. = *Triticum* sp. [only where more specific identifications are not available]; Tt = *Triticum timopheevi;* Tda = *Triticum turgidum/aestivum* (free-threshing); Sc = *Secale* sp.*;* Ca = *Cicier arietnium;* Lc = *Lens* sp./*culinaris*; Ls = *Lathyrus* sp./sativus; Ps = *Pisum* sp./*sativum;* Ve = *Vicia ervilia;* Vf = *Vica faba;* Lu = *Linum usitatissimum.* Crops with evidence for morphological change (semi-domesticates or domesticates) indicated in bold (based on taxonomic species level identifications of the original author and/or domestication status inferred in Asouti and Fuller 2013; Fuller et al. 2014)

been considered in terms of timelines (Fig. 7A-B) that illustrate long-term evolutionary processes within crop species, but here are considered as they correspond to the economic classification levels above, for sites that have both data types available (Fig. 7C-D). Mixed-subsistence economies fall between the yellow bands in Fig. 7C-D. Mixed-subsistence economies are predominant for sites where cereals that are either under incipient or entrenched pre-domestication cultivation, which is also indicated by linear regression analyses. However, there are many outliers. These include a small number of sites that have wild-type cereals in economies that are crop-dominated, i.e., something agriculture-like but with wild-type cereals. Examples include Nevali Çori (with wild-type einkorn rachis), and wild-type emmer grains from early Çayönü (1B), but also Tell Aswad where domestication indicators in terms of barley and emmer rachis and grain size are low to intermediate while the economy is decidedly crop-dominant. Fully domesticated grains occur predominantly in mixed-subsistence and agriculturally-focused economies, but are absent from foraging-focused economies. El Kowm and Abu Hureyra 2B/2C provide the lowest levels of crops for sites with fully domesticated cereals. Based on the extent of grain size increase, Gusir Höyük 2 (20.95% maximum) and Wadi Jilat 7 (9% maximum) have mixed economies with low crop levels despite apparently domesticated cereals. Thus, alongside slow domestication processes is a slow and rather piecemeal trajectory of more and more communities becoming more focused on crops, but there is no horizon that marks a regional "agricultural revolution", nor that links agriculture to the possession of fully domesticated grain crops. Both economic change and domestication are emergent traits of a slower regional process.

In contrast to the expectations of Bellwood (2005, 2017) and Rowley-Conwy (2004) (illustrated in Fig. 2), we find a major dominance of mixed economic systems throughout the Pre-Pottery Neolithic and even into the early Pottery Neolithic (Fig. 8). We thus confirm the contention of Smith (2001) that intermediate states such as lower level food production could be stable strategies for long periods of time. The available data indicates the persistence of "middle ground societies" for around 4000 years in southwest Asia. This is not predicted by the ethnographic data and therefore

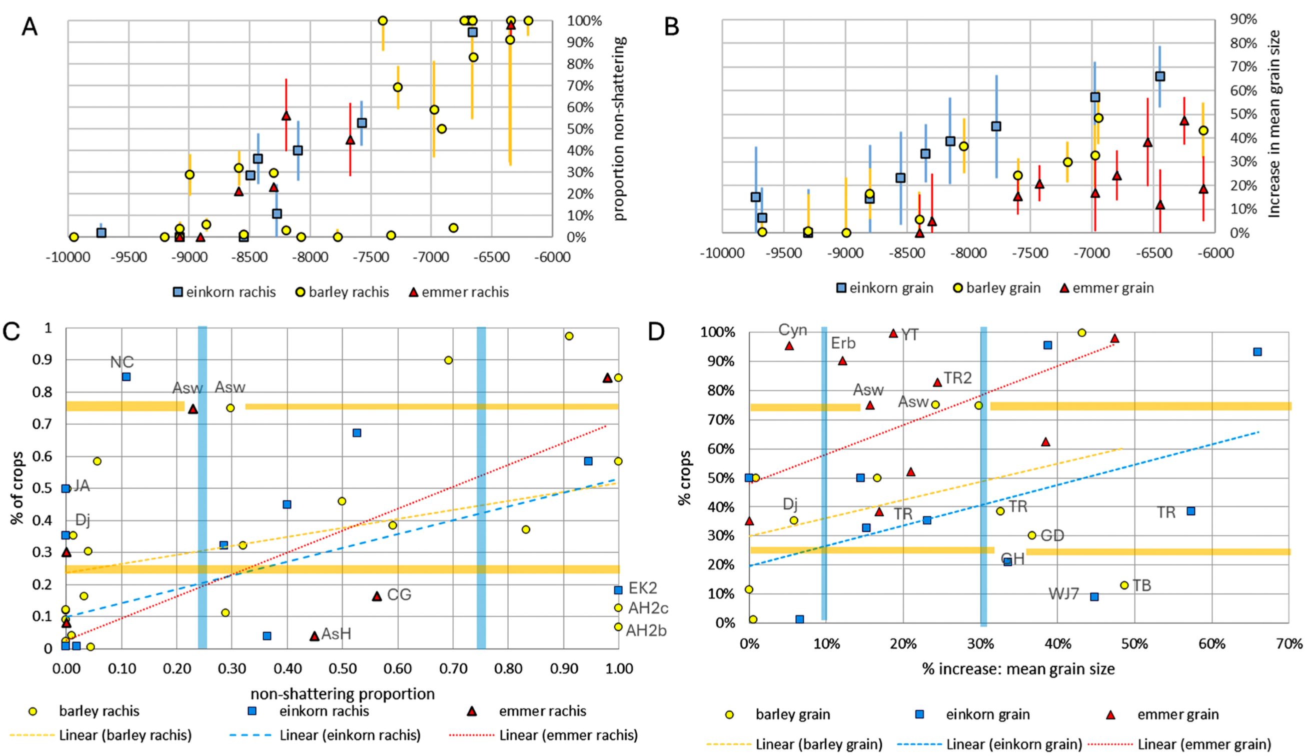

Fig. 7 Comparisons between domestication status and economic status. **A** The timeline view of evolution of non-shattering in cereals, plotted as mean percentage with standard deviation against median age. **B** The timeline of cereal grain size increase, plotted as percentage increase in assemblage mean over smallest mean, with standard deviation of assemblage measurements expressed as a percentage. **C** Domestication status based on proportion of non-shattering rachis data (x-axis) plotted against percentage of crop remains (y-axis) for individual site/phase assemblages. **D** Domestication status based on grain size data (% increase in mean grain thickness/width of cereals) versus percentage of crops in the assemblage. Blue vertical lines divide estimates of domestication process stages: incipient pre-domestication (culti-wilds), entrenched pre-domestication cultivation (semi-domesticates), and domesticated. Horizontal lines indicate lower and upper quartiles in economic reliance on crops.. Dataset: Table S4. Selected sites labelled: NC = Nevalı Çori, Asw = Tell Aswad, JA = Jerf al Ahmar, Dj = Djade, AsH = Aşıklı Höyük, CG = Choga Golan, EK2 = El Kowm 2, AH2 = Abu Hureyra 2 phases, Cyn = Çayönü, Erb = Erbaba, YT = Yarim Tepe, Tell Ramad (including later phase 2), GD = Ganj Dareh, GH = Gusir Höyük, WJ7 = Wadi Jilat 7, TB = Tell Bouqras

confirms the importance of non-analogue economic systems. The Pre-Pottery Neolithic in this region shows a long predominance of mixed-subsistence economies, which are generally linked to the evolution of domesticated morphology, but as indicated in Fig. 5, this is not exclusively the case. It also indicates, however, regional differences in the importance of mixed economies and the establishment of agricultural economies. Based on the current evidence, it is in the Levant -both northern and southern Levantine—that transition into intermediate economies during the PPNA, joined by Northern Fertile Crescent sites from the Early PPNB. However, the Northern Fertile Crescent is first to record crop-dominant assemblages and arguably more agriculturally focused economies, even prior to much evolution towards domestication. Tell Aswad is also precocious in terms of reliance on crops while cereals are still early in their evolutionary process. Cyprus follows its own trajectory in which after an early emphasis on cereals, as well as potentially early livestock, economies through the later Neolithic up to the Early Bronze Age focused more on wild plant foods and game like deer (Lucas and Fuller 2020). Nevertheless, morphological domestication is not associated with the more agriculturally focused sites of the Northern Fertile Crescent, but instead makes a clearer showing in the intermediate economies of the northern and southern Levant, as well as in Cyprus that appears to have had accelerated rates of evolution of domestication traits like grain size (Lucas et al. 2012). Mixed subsistence economies are important in the Eastern Fertile Crescent and Central Anatolia in the Later PPNB and the pottery Neolithic, by which time the Levant and Northern Fertile Crescent are more agricultural and crop dominated.

A role for Caprine pastoralism on agricultural commitment?

Having established a timeline for mixed-subsistence economies and shifts towards agricultural reliance, we can now assess whether there is a correlated change in the importance

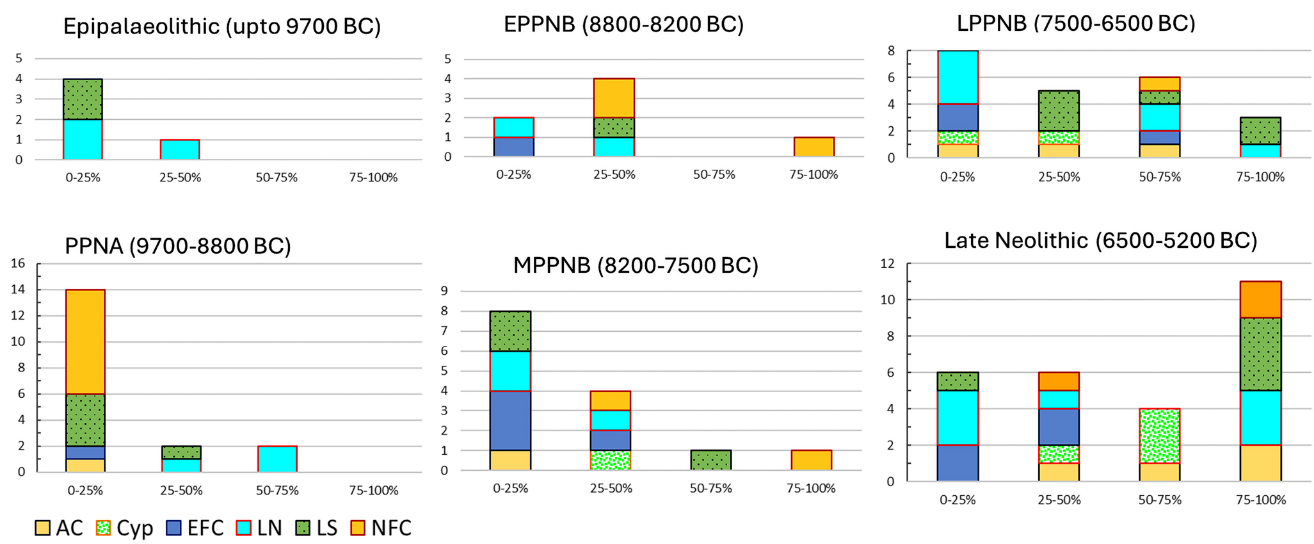

Fig. 8 Histograms of the number of sites with different levels of crops in their archaeobotanical assemblages for the major chronological phases. X-axis indicates proportion of crops out of all reported seed/fruit remains. Only includes sites with assemblages of at least 300 NISP and 10 taxa identified. Dataset: Table S3

of pastoralist production. A number of authors have suggested that an increase in the evolutionary rate of domesticated crops may take place with the advent of herding (e.g. Asouti and Fuller 2012; Allaby et al. 2017; Fuller et al. 2018; Kabukcu et al. 2021), but we suggest here that the relationship may be more about economic change—reliance on cultivation and herding—rather than the evolution of domestication per se. We consider this in a preliminary way in terms of the evidence for sheep and/or goat (caprines), across a selection of sites over time and in relation to the importance of potential crops (Fig. 9). Some early sites with high proportions of caprines likely represent focused hunting on these species within their wild distribution, and we cannot simply equate percentage of *Ovis/Capra* bones with degrees of herding. Nevertheless, we can rely on inferences from zooarchaeologists to differentiate wild from domesticated carpines, which are differentiated by symbology in Fig. 9.

There are also a few sites that have intermediate levels of crops without the presence of many caprines, notably sites

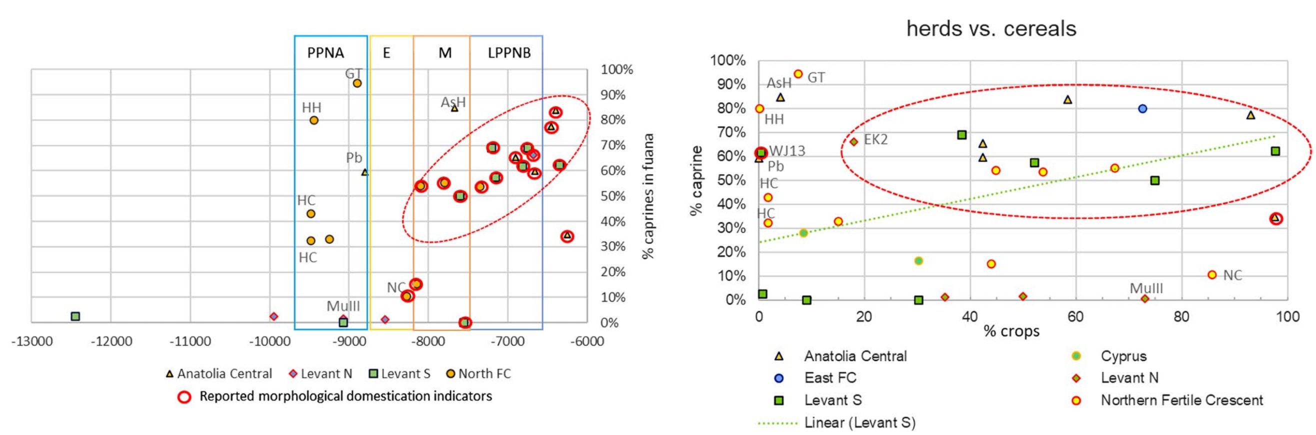

Fig. 9 The relative importance of sheep/goat herding in relation to the timeline of cereal reliance. The proportion of caprines is plotted, regardless of status. Sites for which morphological domestication indicators of caprines have been reported are indicated by a red circular outline. At left the percentage of sheep/goat bone remains plotted against site age. At right, the proportion of caprine bones in relation to the percentage of crops on a site, with linear regression trendline. Dashed red line indicates covariance of crops and caprine proportions among most later sites with domesticated caprines. Selected sites and site groups labelled. Data: Table S5

of the Upper Euphrates with incipient pre-domestication cultivation, such as Mureybit III, Jerf el Ahmar and Dj'ade. Nevertheless, it is apparent that the importance of sheep and goat increases over time, as recognized in most zooarchaeological studies (e.g. Vigne and Helmer 2007; Martin and Edwards 2013; Arbuckle et al. 2014). The most marked jump in caprine presence is around 8000 BC or shortly before, in the MPPNB period when mixed-subsistence economies are well established but on average quite middle of the road in terms of proportion of crops and preceding the rapid upturn in crop importance in the LPPNB. This period is associated with the introduction of domesticated sheep in the southern Levant from an inferred domestication further north as much as 500 years earlier (Martin and Edwards 2013). In this light, it is possible that caprine importance contributed to the conditions that favoured the move to more agricultural economies, as hypothesized by Denham and Donohue (2022). The apparent early exception to this trend comes from sites in the Northern Fertile Crescent, where the upper Tigris hunter-gatherer-fishers likely inhabited habitats rich in wild sheep. Indeed wild sheep and pig, sometimes both, may have been seen as important foci of hunting (Peters et al. 2013; Itahashi et al. 2017; Zeder and Lemoine 2022); Pinarbasi in Central Anatolia, during the equivalent of the PPNA, is a similar case with wild sheep and cattle, hunted alongside small mammals, birds and fish (Baird 2012); plant resources are predominantly wild nuts, grasses and many sedge nutlets (Fairbairn et al. 2014).

For the majority of sites dating after 8500 BC, there is a general correlation between more crops and more caprines: this indicates the evolution of a caprine-herding economy in concert with increasing crop importance. The two aspects of the economy can complement each other, crop waste or crop surplus can feed domestic caprines, while dung from animals penned or near site can manure arable soils. Vigne and Helmer (2007) argue that a central aspect of the new caprine and cattle herding economy between 8500 and 7500 BC was the use of lifetime products, such as milk, while meat was still primarily provided by hunted game. There are a few exceptions to this pattern in which mixed-subsistence economies with culti-wild crops show little evidence for caprines, especially sites in the northern Levant known for pre-domestication cultivation (Mureybit, Jerf el Ahmar, Dja'de). Netiv Hagdud, a southern Levantine PPNA site is similarly mixed-subsistence with culti-wild cereal well in advance of the spread of any livestock. Çayönü and Nevali Çori, in the western part of the Northern Fertile Crescent, which take up significant investment in cultivation in the EPPNB (crop-dominated assemblages with culti-wilds and semi-domesticates), may have only a minor component of early Caprine meat, although morphological domestication processes have been inferred here (Hongo et al. 2005; Peters et al. 2013), and use of milk seems plausible (Vigne and Helmer 2007). The analyses of Peters et al. (2013) suggest that increasing sheep and goat through the sequence at Nevali Çori and Çayönü, together with increasing statistical similarity to later Neolithic assemblages, indicate a trend away from more diverse hunted fauna in the earliest phases towards more reliance on herding (for meat and milk) later on. Later in this same region, Cafer Höyük, has substantially higher proportions of crops (semi-domesticates in mixed subsistence), and substantial proportions of caprines. While some animals may have been herded, it is only later, after Cafer Höyük, when there is recognizable domestication-related size change in the region (Peters et al. 2013). Another set of exceptions are the persistent hunter-gatherers, such as those of the upper Tigris region and Central Anatolia, where crops are absent, apart from some progenitors (especially pulses), and wild caprines (especially sheep) were apparently readily available for hunting; this is within the zone dubbed as the *Ovis-Capra*-zone for early Holocene hunting traditions (Peters et al. 2013). Nevertheless, there are numerous sites in both in the Southern Levant (from the MPPNB onwards) and in Anatolia (mostly from the Late PPNB) which indicate early integration of caprine herding and with increased reliance on cultivation, thus during an era of mixed subsistence economies transitioning toward agriculture. In the Levant and the Western part of the Fertile Crescent this period of herded caprines started during a period of dominance by semi-domesticates (the entrenched pre-domestication cultivation stage of crop evolution), but herded caprines only come to Central Anatolia after most crops are morphologically domesticated. However, it now evident at Aşıklı Höyük and Çatalhöyük, that *Triticum timopheevii* was semi-domesticated alongside herded caprines (Charles et al. 2021); *T. timopheevi* appears to a be a later domesticated wheat species that partly displaced the more evolved emmer and einkorn in this region and period (see Filipović et al. 2023).

Concluding remarks

On the basis of empirical evidence, we can reject the equation of pre-domestication cultivation with low-level food production, just as we can reject the notion of a rapid economic transition or an unstable "substitution phase" (sensu Rowley-Conwy 2004; Bellwood 2005), at least in the context of agricultural origins in Southwestern Asia. Instead, we see a diversity of mixed-subsistence economies in the Levant (north and south) and northern Fertile Crescent starting in the PPNA and continuing through the Late PPNB. The diversity of these economies represents several non-analogue socioeconomic systems, which need to be understood on their own terms through archaeological evidence and are not readily modelled by analogy with ethnographic models for village farming or small-holders (Asouti and Fairbairn 2010). For the most part this economic diversity persists through the incipient and entrenched pre-domestication cultivation phases, and even alongside fully domesticated crops. The early stages of the evolution of non-shattering cereals can be found on sites with foraging-focused economies as well as mixed-subsistence economies, and even a few crop-dominated sites known from the later PPNA in the western part of the Northern Fertile Crescent. Grain size increase is most evident only in sites that had begun mixed-subsistence economic forms of investment (Fig. 6). While non-shattering and grain size are known to evolve for different reasons, one connected to harvesting cycles and the other to soil conditions of sowing (Fuller et al. 2014; Allaby et al. 2022a, b), these patterns suggest some differences in terms of socio-economic context. Persistent selection for large grain sizes may be more likely in situations where cultivation was more important to the economy and thus more intensive and more routine. Interestingly, during the PPNA period, sites in the eastern part of the Northern Fertile Crescent, or at least its eastern portion, seem outside the regions with practices of early cultivation. However, by the Early PPNB, cultivation was taken up, suggesting a process of the spread of early cultivation and crops (still morphologically wild) into the region. (e.g. Savard et al. 2006, Colledge et al. 2004, Arranz-Otaegui et al. 2016a). Genetic data suggests such flows of crops were not unidirectional but multi-directional, creating what were ultimately domesticated populations that drew from geographically dispersed wild populations (Allaby et al. 2022a; Fuller et al. 2023).

Recent data from Gusir Höyük, for example, is emblematic of this (Kabukcu et al. 2021). Wild cereals are absent from the first two phases (PPNA) and appear in the EPPNB (Phase 3) by ca. 8400 BCE, with no sign of non-shattering morphology, but with an increase in mean grain size of just over 30%, comparable to nearby contemporary sites like Çayönü (Channel phase) to the west and Dja'de (Northern Levant). This suggests the introduction of cereals under pre-domestication cultivation that had begun evolving elsewhere. Further east the appearance of emmer wheat at Chogha Golan in horizon 2, ca. 7800 BCE (Riehl et al. 2015), with ~ 56% non-shattering rachis (based on the small identifiable sample, Weide et al. 2015), would be further evidence for the spread of semi-domesticates. This suggests inter-regional connections to the northern Levant, where despite the importance of cultivation, non-shattering evolved rather later than contemporary sites further South (Allaby et al. 2017); as noted above we find some indication that grain size and non-shattering may have been under stronger selection in different regions. It was only later, with inter-regional processes of interaction and gene flow, that the metapopulations of the cereals became more uniformly domesticated (see Allaby et al. 2022a).

Although a few sites appear to be leaning towards an agricultural economy in the Middle and Late PPNB, these are exceptions in the overall pattern. Instead, it is only in the Late or Ceramic Neolithic that agriculturally focused economies are the norm and widespread (Fig. 7). Therefore, in general terms we can point to domestication becoming largely fixed in genetic terms in cereals, and presumably pulses (judging by size change), around the start of the Late PPNB, whereas the transition to agriculture took place around the end of the Late PPNB. Incipient pre-domestication cultivation had started 3000–4000 years earlier. Recently, Weide et al. (2022), have questioned just how systematic this cultivation was (but see Willcox 2023, 2024), but it seems likely to have varied across sites and regions, with more routine efforts of cultivation creating hotspots for selection of domestication traits within a wider landscape of variable human impacts on wild progenitor populations (see Allaby et al. 2022a; Fuller et al. 2023). However, it is the entrenchment of the evolutionary trends in crop morphology from various times within the Early and Middle PPNB (varying by crop and across sites and regions), when systematic and intensifying cultivation is clear, pushing the evolution of domestication traits along, but these processes may have been stronger in some hotspots for some crops or domestication traits. Domestication processes in themselves did not necessarily lock communities into agricultural economic systems, but there continued to be a wide diversity of levels of reliance on crops. Early crops, culti-wild or semi-domesticated, were being dispersed quite widely by this time. Domestication was clearly not fixed when crops were undergoing early dispersal around the region, facilitating the potential mixing of early crops from different wild populations. Economies remained varied; these can be seen as multiple experiments in balancing cultivation, gathering, and hunting, and it was millennia before agricultural commitment emerged as the dominant economic system. The increasing adoption of, and investment in, animal herds, and reliance on sheep and/or goat, appears to have provided additional incentive for increasing economic reliance on cultivation.

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