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Alexander Weide, Laura Green, John Hodgson, Carolynne Douché, Margareta Tengberg, et al.. A new functional ecological model reveals the nature of early plant management in southwest Asia. *Nature Plants*, 2022, 8 (6), pp.623-634. 10.1038/s41477-022-01161-7 . hal-03941959

HAL Id: hal-03941959

<https://hal.science/hal-03941959>

Submitted on 7 Feb 2024

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A new functional ecological model reveals the nature of early plant management in southwest Asia

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Abstract

The protracted domestication model posits that wild cereals in southwest Asia were cultivated over millennia prior to the appearance of domesticated cereals in the archaeological record. These ‘pre-domestication cultivation’ (PDC) activities are widely understood as entailing annual cycles of soil tillage and sowing, and expected to select for domestic traits such as non-shattering ears. However, the reconstruction of these practices is mostly based on indirect evidence and speculation, raising the question whether PDC created arable environments that would select for domestic traits. We developed a novel functional ecological model that distinguishes arable fields from wild cereal habitats in the Levant using plant functional traits related to mechanical soil disturbance. Our results show that exploitation practices at key PDC sites maintained soil disturbance conditions similar to untilled wild cereal habitats. This implies that PDC did not create arable environments through regular tillage but entailed low-input exploitation practices oriented on the ecological strategies of the competitive large-seeded grasses themselves.

1. Introduction

The protracted domestication model for the origins of plant cultivation and domestication in southwest Asia posits that wild cereals and pulses were cultivated for at least 1000-2000 years prior to the appearance of morphologically differentiated domesticated crops in the archaeological record¹⁻³. Snir *et al.*⁴ even suggested wild cereal cultivation around the Last Glacial Maximum, 23,000 years ago, at Ohalo II on the Sea of Galilee. This prolonged phase of wild plant cultivation is termed ‘pre-domestication cultivation’ (PDC) and inferred through different lines of evidence, including large quantities of cereal or pulse grains^{1,5}, increased grain sizes⁶⁻⁸, the presence of substantial storage facilities^{9,10}, and the occurrence of crop progenitors outside of their natural distribution range¹. The most direct evidence to suggest wild plant cultivation is, however, based on genera that include arable weed species^{1,4,7,8,11-13}. Associations of seeds and fruits from these potential arable weed genera with large amounts of wild cereal and pulse remains at archaeological sites are commonly interpret-

ed as indicative of increased levels of disturbance due to vegetation clearance and soil tillage¹¹⁻¹³, which generally feature as the defining aspects of cultivation as a subsistence practice¹⁴. This highlights that the formation of early arable weed floras is thought to reflect agricultural disturbances, as opposed to other common disturbance factors in Mediterranean grasslands like summer-droughts, grazing, and wildfires¹⁵. The increased sizes of wild cereal grains at some sites are also conventionally attributed to soil disturbance, due to the expectation that larger grains and their large seedlings have competitive advantages in open environments and when buried deeper^{16,17}. Although cereal grain size increases were possibly related to other factors as well, such as variable water availability when sown on different soils or fluctuating levels of atmospheric CO₂ during the Early Holocene^{1,18}, most authors attributed the combination of potential arable weeds and increasing grain sizes to cultivation in disturbed arable habitats. PDC is therefore understood, often explicitly, as entailing relatively labour-intensive practices comparable to developed agricultural systems, including vegetation clearance and annual cycles of soil tillage, sowing, probably weeding, and harvesting^{5,10-12,17}. This current understanding of PDC diverges from other models for emerging plant management practices around the world, which emphasise the viability of low-input strategies for facilitating the abundance of exploitable resources that do not rely on increased levels of disturbance¹⁹⁻²¹. Importantly, associating labour-intensive agricultural practices with PDC has profound socio-economic implications because tillage demands increased inputs of labour and energy into units of land from which food is obtained. Increasing social complexity and labour inputs into arable land therefore feature as fundamental socio-economic developments entangled with the emergence of domesticated crops^{17,19,22}.

This traditional reconstruction of PDC assumes that wild cereals and pulses were cultivated in relatively disturbed arable environments for millennia without genetically fixing central domestication traits. Many scholars perceived this as a theoretical paradox because the continuous harvesting and sowing of annual plants should induce selection for key domestic traits such as non-shattering cereal ears^{1,11,18}. For the southwest Asian cereal domesticates, this expectation is in part based on the fa-

mous cultivation experiments by G.C. Hillman and M.S. Davies²³, who showed that annual cereal cultivation that employs harvesting techniques like uprooting or sickle reaping would automatically select for non-shattering ears and could theoretically lead to a non-shattering population in decades or a few centuries. The millennia-long PDC phase contradicts this hypothesis, also as the use of sickles as harvesting tools is well attested archaeologically during the Late Pleistocene and Early Holocene³. To resolve this discrepancy between archaeological observations and theoretical expectations, researchers have proposed various scenarios to explain why the proportions of non-shattering spikelets never exceeded that of modern wild populations despite millennia of PDC. These include harvesting semi-ripe ears to prevent grain loss through shattering, ground collection of shed spikelets to maximize yields, the continuous cultivation of wild cereals in the same fields, where the shattered spikelets contribute significantly to the population in the following year, and collecting grains from unmanaged populations for replenishing seed stocks after failed harvests^{1,17,23,24}. All these strategies would maintain high proportions of shattering spikelets in the managed populations, suppressing selection for non-shattering phenotypes. Alternatively, Asouti¹⁸ suggested that plant cultivation would not have been a resilient strategy during the climatically unstable Early Holocene, prompting human communities to frequently focus on alternative resources which would have interrupted and possibly reversed selection for domestication traits. However, except for harvesting semi-ripe ears³, all these explanations are speculative and not based on direct archaeological evidence. As a result, specific practices associated with PDC, and their socio-economic significance, remain unknown, as do the factors that inhibited selection for domestication traits during millennia of PDC. Weide et al.²⁵ provided empirical evidence which suggests that the conventional taxonomic approach to identifying early arable weed floras, and with this the emergence of cultivation systems that involve regular soil disturbance, is fundamentally flawed. Many arable species originated in non-arable southwest Asian grasslands that are dominated by cereal crop progenitors²⁶. Consequently, the seeds and fruits of potential weed genera at key PDC sites could likewise derive from non-arable species or facultative weeds harvested with wild cereals in local non-arable grasslands^{25,27,28}. If the

associated exploitation practices did not include annual cycles of tillage and sowing but rather focused on strategies that maintained low levels of disturbance and relied on self-sowing of the targeted species, the absence of selection for domestication traits would be expected rather than being anomalous²³. To test whether the proposed weed floras from Late Pleistocene and Early Holocene PDC sites reflect such non-arable grassland communities, we need to reconstruct disturbance levels much more precisely than is possible with the taxonomic approach currently used. Analysing the composition of plant functional traits related to agroecological variables such as mechanical soil disturbance offers a promising solution to these problems and has proven useful in reconstructing management regimes and associated practices in the past^{29,30}.

Distinguishing arable from non-arable habitats using functional ecology

Plant functional traits occur in limited sets of combinations globally³¹ and can be used to assess, for example, how ecological parameters affect species distribution and determine community assembly³². In applying functional ecology to arable weed floras, certain sets of functional traits successfully distinguished between relatively high- and low-intensity cultivation regimes in temperate and Mediterranean Europe, northern Africa, and in archaeological contexts^{30,33-36}. Moreover, our functional ecological approach is suited to overcoming shortcomings of the conventional taxonomic approach to the identification of early cultivation and associated practices. First, functional analyses of archaeobotanical assemblages are based on species from individual samples or contexts rather than an arbitrary selection from all identified *potential* weed taxa of a site^{33,37}. This has the advantage of selecting weed species based on their co-occurrence with crops or target species that dominate individual samples, which does not *a priori* exclude edible weed species and results in a more accurate identification of ancient weed floras. Second, in building a functional model based on modern survey data, we can differentiate ecological conditions along a continuous spectrum and locate archaeobotanical samples along this ecological continuum. As opposed to the conventional taxonomic approach, this goes beyond the dichotomous distinction between gathered and cultivat-

ed archaeobotanical assemblages. Third, these sample-by-sample functional analyses provide a reliable estimate of the variability of practices within a prehistoric human community and the opportunity to analyse this variability in its specific socio-economic context and over time³⁶.

The modern arable weed floras analysed in this study (Fig. 1) developed under ‘traditional’ husbandry regimes in Palestine during the first half of the twentieth century as part of the *musha’a* land tenure system (Zohary 1950). The *musha’a* was characterised by two-field rotation with a winter cereal or legume on one field and a summer crop of sesame or durrah (*Sorghum bicolor*) on a second field that remained fallow during the rainy period^{26,38}. Irrigation and manuring played limited roles, but fallow fields were tilled up to three times during the fallow period using animal-drawn ards (or ‘scratch-plows’)³⁹. The sampled non-arable habitats (Fig. 1; Table 1) are all dominated by southwest Asian cereal crop progenitors (*Hordeum vulgare* subsp. *spontaneum*, *Triticum turgidum* subsp. *dicoccoides*) and related, large-seeded grasses (*Aegilops geniculata*, *Ae. peregrina*, *Avena sterilis*, *Hordeum bulbosum*). None of the sampled wild cereal habitats were cultivated during the last ca. 50 years; nor were they exposed to regular grazing, which reduces the density of wild cereal stands and selects for shorter small-seeded species^{40,41}. The only exceptions are Karei Deshe, with a medium stocking rate of 0.55 cows per hectare, and Lehavim, where a flock of ca. 600 sheep continuously grazed plots during winter/spring, resulting in a reduction of large-seeded grasses (see Methods section).

Here we use flowering duration and the ability of perennials to readily regenerate from root and rhizome fragments, traits that are positively related to high levels of mechanical soil disturbance^{29,30}, to build a functional ecological model that differentiates between disturbance regimes of the surveyed arable and non-arable habitats (Supplementary Table 1). Annual and perennial species that flower rapidly and over an extended period have a higher probability of regenerating from seeds in regimes of high disturbance¹⁵. Similarly, perennials that rapidly regenerate from root and rhizome fragments perform well under conditions of high mechanical disturbance, which even facilitates their growth⁴². These traits were related to conditions of high mechanical disturbance in different climatic and eco-

logical settings, including England³⁵, Greece³⁰, Spain⁴³, and Morocco³⁴, demonstrating that they function independently from local environmental conditions and are applicable to archaeological contexts³³⁻³⁵.

We apply the functional model to seven archaeobotanical datasets dating to the Early Epipalaeolithic (EP), the Pre-Pottery Neolithic (PPN) and the Pottery or Late Neolithic (LN). The sites include Ohalo II (EP, ca. 23,000 cal. BP), Gilgal I and Netiv Hagdud (PPNA, ca. 11,500–10,800 cal. BP) in the Jordan valley and Jerf el Ahmar and Dja'de (PPNA–early PPNB, ca. 11,350–10,240 cal. BP) on the Middle Euphrates (Fig. 1). All these sites were interpreted as reflecting PDC, primarily based on potential weed floras, together with large amounts of wild cereal and pulse remains and substantial storage facilities^{1,4,5,9,10,13}. The analysed samples are dominated by wild cereals and are representative of ecological conditions in cereal stands with the exception of samples from Dja'de (phases II+III), where pulses dominate most samples (Supplementary Fig. 1-5; Supplementary Tables 2-3). We contrast the disturbance regimes of these key PDC sites with those of fully established farming communities at Atlit-Yam (PPNC, ca 9,200–8,500 cal. BP) in Israel and Çatalhöyük (LN, middle and late phase of the site, ca 8,650–8250 cal. BP) in central Anatolia, where the comparatively intensive cultivation of domesticated crops involving regular soil tillage is expected (Supplementary Fig. 6; Supplementary Tables 2-3)^{36,44}. We correlate the development of ecological disturbance regimes with archaeological structures that are widely used as key markers for socio-economic change, including house architecture and storage practices^{45,46}. In addition, we discuss the implications of our findings in light of recent advances in understanding the adaptive syndrome of large-seeded crop progenitors^{28,47}, which urges us to shift the inherently anthropocentric focus in explaining early cultivation practices and selection for domestication traits to the exploited plant species and their ecological strategies.

2. Results

Distinguishing modern wild cereal habitats from arable fields

Modern arable weed floras and wild cereal communities in the Mediterranean and Irano-Turanian phytogeographical regions of the southern Levant were clearly separated based on species composition (Fig. 2a). A detrended correspondence analysis (DCA) using semi-quantitative data (species presence/absence), based on 156 samples (transects and plots) from arable fields ($n=61$) and non-arable wild cereal habitats ($n=97$) with 150 species, separated both groups along axis 1. Weide et al.²⁵ showed that this clear separation is based on the ecological conditions in the arable and non-arable habitats, related to local land-use practices, and is not induced by different survey periods or methods. The floristic variation within both groups reflects a combination of factors related to topographic and edaphic conditions and differences in the local vegetation^{25,26}. Coding species according to the duration of their flowering period shows that long-flowering species (>5 months) occur in higher proportions in the arable fields compared to the non-arable grassland communities, which support more short-flowering species (<3 months) (Fig. 2b). Figure 2c shows that perennials which readily regenerate from root and rhizome fragments also reach higher proportions in the arable fields, confirming that readily regenerating and long flowering species are suited to indicate differences in disturbance conditions between arable and non-arable habitats (see Supplementary Figure 7 for species plots of the DCA coded according to the two functional traits).

We used discriminant analysis (DA) to distinguish between the modern arable and non-arable communities based on semi-quantitative data (presence/absence). In a first DA we used flowering duration and vegetative regeneration as the discriminating variables (DA1; Supplementary Table 4). Supplementary Fig. 8a shows the discriminant function extracted from DA1 that correctly reclassified 90.2% of all modern samples. The two traits discriminate between arable and non-arable communities as predicted, with arable weed floras characterised by species that regenerate from vegetative organs fragmented by tillage (roots, rhizomes) and/or seeds produced before a mechanical disturbance event such as tillage or weeding disrupted their life cycle (flowering duration) (Supplementary Fig. 8b). A small number of samples was incorrectly reclassified as deriving from either a non-arable grassland community ($n=6$ or 9.8% of arable fields) or an arable field ($n=7$ or 9.9% of non-arable

samples) (Supplementary Table 4). This overlap in disturbance conditions indicates that arable and non-arable habitats in the Southern Levant represent an ecological continuum rather than categorically distinct environments. Moderate to heavy grazing did not affect the correct reclassification of samples from Karei Deshe and Lehavim, although it explains higher disturbance levels as seen in the higher discriminant scores of the samples from grazed plots at Lehavim compared to the ungrazed plots from the same site. The separation of arable and non-arable habitats on the discriminant function therefore primarily reflects the presence and varying intensity of soil tillage.

One disadvantage with using this combination of traits is that samples without perennials are omitted from the analysis as they did not receive an attribute score for vegetative regeneration. This excluded 26 samples from non-arable habitats, including 63% of the samples from Lehavim. We therefore repeated the DA with flowering duration as the only discriminating variable (DA2). The discriminant function extracted from DA2 correctly reclassified 86.7% of all samples and maintained the general trends of all sample groups (Fig. 3a; Supplementary Table 4). The number of samples incorrectly reclassified increased among the arable fields ($n=9$ or 14.8%) and grasslands ($n=12$ or 12.4%) (Table 2). Moderately to heavily grazed plots were again correctly reclassified as non-arable, confirming that both functions discriminate between communities in tilled and non-tilled habitats independently from local grazing regimes.

Disturbance regimes associated with pre-domestication cultivation

The two extracted discriminant functions were used to classify archaeobotanical samples from seven sites that span the proposed origin of PDC activities to the establishment of relatively intensive, mixed farming systems (Table 2; Fig. 3; Supplementary Figure 8; Supplementary Table 4). The two functions classified 90.5% (DA1) and 87.9% (DA2) of samples from Çatalhöyük as arable and the majority of samples from Jerf el Ahmar (DA1: 87.5%; DA2: 85%) and Netiv Hagdud (100% in both DAs) as non-arable. The weed community associated with stored wild cereals at Gilgal I was classified as non-arable in both DAs. For Ohalo II, excluding the species likely used for the grass bedding and the

hut construction leads to a classification of the community as non-arable in both DAs, because taxa possibly collected as construction material include relatively long-flowering species (*Atriplex rosea*, *A. leucoclada*, *Suaeda fruticosa*)⁴⁸. The selection of potential arable weeds used by Snir *et al.*⁴ to suggest wild cereal cultivation at Ohalo II only contained annuals and was classified as non-arable based on flowering duration only (DA2).

DA1 omitted almost half of all archaeobotanical samples (41 of 98), as they did not contain perennials. This included the majority of samples from Dja'de (69%) and Atlit-Yam (75%), and a large proportion from Çatalhöyük (36%), making it impossible to compare sample variance and the relative position of sites on the discriminant function. DA2 classified 87.9% of samples from Atlit-Yam as arable and 88.5% of samples from Dja'de as non-arable (Table 2; Fig. 3). Although this discriminant function is less powerful in discriminating between communities from tilled and non-tilled soils, it confirms that the assemblages from the PDC sites of Ohalo II, Netiv Hagdud, Gilgal I, Jerf el Ahmar, and Dja'de all correspond to disturbance levels found in modern untilled wild cereal habitats, whereas Çatalhöyük and Atlit-Yam clearly reflect increased soil disturbance in established agricultural systems. As the Neolithic sites were situated in different environmental and climatic zones, this clear trend towards increased disturbance conditions at the younger agricultural sites suggests that flowering duration functions as a reliable indicator for agricultural disturbances in the early Holocene. Table 3 gives the centroids (means), variance, and standard deviation for the archaeological datasets, showing that the farming communities at Çatalhöyük and Atlit-Yam produced more variable disturbance conditions than the earlier PDC sites. For Çatalhöyük, Green *et al.*³⁶ plausibly attributed variability in crop growing conditions to household-level decision making and variable proximity of households to productive arable land.

The proportions of samples from Çatalhöyük and Atlit-Yam reclassified as non-arable in both DAs (DA1: 8.7%; DA2: 12.5%) correspond well to the proportion of modern weed floras incorrectly reclassified as non-arable communities (DA1: 9.8%; DA2: 14.8%). We see a similar pattern at Dja'de and Jerf el Ahmar, where 11.5% and 15% of samples, respectively, were classified as arable in DA2.

These proportions broadly correspond to the percentage of samples from modern untilled grassland communities incorrectly reclassified as arable weed floras (12.4%), urging caution in interpreting these samples from Dja'de and Jerf el Ahmar *per se* as indicative of regular tillage. The three samples classified as arable from Dja'de consistently received positive discriminant scores beyond the range of modern untilled grassland communities, indicative of increased soil disturbance. Two of these three samples date to the last documented occupation phase at the site and are dominated by lentils (Fig. 3d). However, such 'high disturbance' outliers also occurred among the modern untilled grassland habitats, suggesting that the increased soil disturbance can be related to other factors than tillage.

Samples from Jerf el Ahmar show no increase in discriminant scores throughout the three occupation phases, with the only positive outlier dating to the earliest occupation phase (Fig. 3e). The documented size increase in barley and einkorn grains throughout the occupation of the site⁶ therefore seems to be related to factors other than deeper burial conditions in tilled soils, supporting recent studies that raised doubts over a general relationship between soil disturbance and selection for larger seeds⁴⁹. Large-seeded phenotypes have strong competitive advantages under conditions of high interspecific competition due to their higher germination success and larger plant size⁵⁰. Under conditions of relatively low soil disturbance, selection for larger seeds could in part be linked to these competitive advantages gained through seed size enlargement, resulting in larger seedlings that can more optimally exploit the increasingly productive conditions during the Early Holocene and surrounding human habitations⁵⁰.

3. Discussion

The ecology of pre-domestication cultivation

In ecological terms, vegetation clearance and soil tillage have the primary goals of establishing an arable field that gives the sown grains a competitive advantage and release resources for growth^{14,51}.

The fact that human communities at key PDC sites did not regularly till the soils from which they

harvested wild cereals indicates that their exploitation strategies did not require frequent mechanical disturbance of the soil and the complete removal of competing vegetation to favour wild cereals. We suggest that this is due to their adaptive syndrome, summarised recently by Wood and Lenné²⁸ as consisting of large seeds in awned spikelets that facilitate quick burial in the soil and contribute to the ability of the wild cereals to form dense stands and dominate annual grasslands. A key trait of this adaptive syndrome is the comparatively large size of the grains of cereal crop progenitors, which produce large seedlings that are very competitive and provide a high fitness in annual plant communities^{47,50}. The key to understand the low disturbance levels in the exploited wild cereal habitats therefore is that regular soil tillage and the clearance of vegetation would not be necessary for giving wild cereals an advantage over other species. These patterns suggest that human communities at sites such as Jerf el Ahmar, Dja'de, Netiv Hagdud, or Gilgal I based their strategies of maintaining rich and exploitable wild cereal populations on the ecological strategies and the high competitiveness of the cereals themselves. This may have included the active re-sowing of stands and their protection from large grazers, practices that are widely documented ethnographically²⁰. In addition, our findings illustrate that the potential weed floras that accompany wild cereals in archaeological contexts do not represent arable communities but rather the floristic composition of untilled grasslands, harvested together with the cereals²⁵.

Low levels of mechanical disturbance associated with 'pre-domestication cultivation' do not automatically explain the absence of selection for domestication traits, because annual cycles of sowing and harvesting could impose selection pressures even in the absence of frequent soil tillage²³. However, annual sowing is a mere expectation of the PDC model and not evidenced by independent data. On the contrary, P. Anderson argued that annual sowing is by no means necessary to maintain rich wild cereal stands⁵². This is based on field observations, including harvesting of wild cereal stands in Syria and the establishment of an experimental wild cereal population in France. In both contexts, self-sowing of shattering phenotypes was sufficient for producing a rich stand in the year after the population was harvested. Combined with the low disturbance levels associated with PDC

assemblages, these observations suggest that an annual cycle of tillage and sowing was not required to exploit and maintain cereal populations in the vicinity of the analysed sites. This explains the low proportions of non-shattering spikelets in PDC assemblages because the recovery of the exploited populations would primarily be based on grains from shattering phenotypes - even if sowing took place every few years.

Our revised PDC model not only anticipates low selection rates during millennia of cereal exploitation, but also places the ecological strategies of cereals at the centre of modelling the economic strategies of early sedentary communities. In this process, the highly competitive large-seeded cereals must be seen as key agents in shaping human-cereal relationships that could persist over millennia without labour-intensive investments in the creation and maintenance of arable plots.

These findings urge us to reconsider the concept of 'pre-domestication *cultivation*' in southwest Asia as the beginnings of arable farming. Instead, it is plausible to assume that the associated 'low-disturbance' or 'no tillage' management practices were oriented to the ecology of existing cereal populations and aimed at creating and maintaining dense populations. Comparable ecological models exist for the development of close human-plant relationships all around the world⁵³⁻⁵⁵, highlighting that emerging domestication processes are generally grounded in ecological collaborations between humans and other organisms^{21,56}.

Disturbance as a function of socio-economic change

Tillage is a labour-intensive agricultural practice with profound ecological consequences, which is why it features as a key innovation in evolutionary models for the emergence of socially complex farming societies, for example in those developed by D. Harris and refined by D. Fuller^{14,17,19}. Sites such as Jerf el Ahmar and Dja'de, with their evidence for large-scale cereal exploitation, *potential* arable weed floras, and increased cereal grain sizes, can be understood as 'type sites' for the developed stage of PDC that entailed labour-intensive practices including systematic tillage^{10,13}. Our results contradict these expectations, suggesting that regular tillage developed much later than previ-

ously assumed. We argue, however, that this accords much better with the socio-economic organisation of the analysed PDC communities.

At Jerf el Ahmar, several subterranean circular structures indicate the construction of communal buildings where food resources were stored in clay storage bins (Fig. 3e)¹⁰. The last communal building constructed at Jerf el Ahmar did not contain storage bins anymore and the mode of food storage during the final occupation phase is generally unclear, echoing the situation at Dja'de (Fig. 3d)^{57,58}. The 'kitchens' at Jerf el Ahmar, rooms with accumulations of food processing and preparation implements that are only found in some buildings, further indicate that food storage, processing, and consumption retained a strong communal element¹⁰. All these patterns reflect a strong focus on communal social and economic activities on the Middle Euphrates.

Excavations at Gilgal I and Netiv Hagdud revealed structures that imply a comparable focus on communal socio-economic strategies in the Jordan valley. These include structure 11 at Gilgal I, a non-residential building that contained the large hoard of stored barley and oat grains included in our functional analyses (Fig. 3f)^{5,59}, and possible clay storage silos with diameters between 1–3m at Netiv Hagdud (Fig. 3g)⁶⁰. That the structures from Netiv Hagdud represent extramural storage silos is supported by the discovery of comparable silos with suspended floors at Dhra' and Wadi Faynan 16 on the eastern side of the Jordan valley, indicating a regional pattern where extramural silos were used as communal granaries^{8,9}. These silos, together with the location of food processing and preparation facilities inside and outside of residential structures⁶¹, likewise suggest a communal organisation of cereal exploitation, storage, processing, and consumption activities at key PDC sites in the southern Levant⁹. The general absence of grave goods and a lack of indicators for the individual accumulation of material wealth during much of the Levantine PPN situate this communal organisation of cereal exploitation in a pan-regional socio-economic system that strongly emphasised group cohesion and identity at the expense of individuality⁶². In this light, the absence of systematic tillage in communally organised cereal exploitation systems also reflects a lack of social and economic incentives to in-

vest higher amounts of labour into subsistence practices, as individual persons or families would not have benefitted from increased labour investments⁶³. This changed with the gradual emergence of household-centred farming communities from the early and middle PPNB, between ca. 10,700–9,500 cal. BP, which developed increasingly ‘private’ systems of food storage, processing, and consumption^{46,61,64}. The increased levels of soil disturbance at Çatalhöyük reflect a developed phase of this intensification of crop cultivation, where individual households stored their own harvests and directly benefitted from their investments into agricultural labour (Fig. 3b)^{36,46}. Increasing labour investments and the associated acceleration of soil disturbance conditions can therefore be seen as a function of limited sharing networks and emerging ‘private’ ownership over cultivated foods in early farming societies.

4. Methods

Study sites and survey methods

We analysed floristic and functional trait data from non-arable wild cereal habitats and arable fields in the Mediterranean and Irano-Turanian phytogeographical regions⁶⁵ of northern and central Israel. The eight wild cereal habitats have a Mediterranean climate but differed in their long-term mean annual precipitation, elevation, and the dominant grass species (Tab. 1). They were selected based on several criteria: the presence and dominance of at least one large-seeded grass species, the absence of cultivation during the last ca. 50 years and regular grazing. The only exceptions to this were Karei Deshe near the Sea of Galilee and Lehavim in the northern Negev (see below). Survey methods and periods differed between the wild cereal habitats (see also Weide *et al.*²⁵). At Nahal Amud, Rosh Pina, Mt. Gilboa, Gamla, and Ramat Hanadiv (Fig. 1b), we surveyed the vegetation in plots following the method described by Jones *et al.*⁶⁶ and adjusted by Bogaard *et al.*³⁴. In each plot we recorded all species in five 1m² quadrats along a linear transect. In contrast to arable fields, the extent of the surveyed plots is defined by the local topography (roads, rock outcrops) and changes in the vegetation (forest margins). Oriented on these natural boundaries, we placed the 20-

70m long transects along the longitudinal axis of the studied plots and away from roads and forest margins to avoid edge effects. The surveyed area at Gamla represents the only exception to this layout, where we surveyed one 0.23 ha large plot and placed five quadrats each in isolated patches of dense *Triticum turgidum* subsp. *dicoccoides* (GAM-01) or *Avena sterilis* (GAM-02) stands.

From the surveys conducted at Karei Deshe Experimental Farm, located north of the Sea of Galilee near Chorazim (Fig. 1b), we selected survey data from two plots of 31.1 and 28.2 ha. These plots were sampled each year between 2014-2019 and had a continuous moderate stocking rate (0.55 cows ha⁻¹ year⁻¹). The vegetation was sampled along four and five transects, respectively, using the step-point method⁶⁷. It has been acknowledged that this method misses rare species and can underestimate species richness⁶⁸, however, as we describe below, for the statistical analyses we excluded rare species from all datasets.

The selected plots from the long-term ecological research (LTER) site of Kedoshim Forest in the Jerusalem Mountains (Fig. 1b) represent cleared plots in a *Pinus halepensis* plantation⁶⁹. The four 20*20 m plots we selected for this study were completely cleared from trees in 2009 and sampled in 2011 and 2014. All species were recorded using a nested sampling strategy in each 10 m² corner of the four plots, with scales of 10*10 cm, 30*30 cm and 1*1m.

The selected dataset from the LTER site of Lehavim in the Goral Hills, northern Negev (Fig. 1b), derives from eight 10*10 m plots located on the wadi shoulders. Four plots were protected from grazing during the entire survey period between 1996-1999, whereas the other four plots were continuously grazed by a flock of ca. 600 Awassi sheep between January–May and August–December⁷⁰. This heavy grazing pressure resulted in the reduction of large-seeded grasses, such as *A. sterilis*, *Hordeum vulgare* subsp. *spontaneum*, and *T. turgidum* subsp. *dicoccoides*. Every year, all species were recorded in four to five 20*20 cm quadrats per plot.

We used M. Zohary's arable weed surveys as a comparative dataset for local arable environments²⁶ (Fig. 1b). Zohary surveyed arable fields in Mandatory Palestine during the first half of the twentieth century, where he recorded relevés covering a total of 100m² per field. The fields were managed as

part of the *musha'a* land tenure system, which involved tilling of fields up to three times during the fallow periods³⁸. These 'cultivated' or 'bare' fallows are thought to maintain productivity under semi-arid conditions by enhancing soil water retention, fertility, and controlling competition with weeds^{39,51}. The most common tillage implements used in the region during the sampling period were animal-drawn ards, also called scratch ploughs, which were used to till fields in remote and hilly locations, whereas tractor ploughing was restricted to lowland arable fields^{26,39}. However, tractors were only introduced to Mandatory Palestine during the 1920s and did not play a large role in the local *musha'a* during the sampling period⁷¹, indicating that the sampled arable weed floras formed under non-mechanised tillage regimes. Zohary divided the recorded weed floras into associations characteristic for a particular environmental setting. We used his detailed survey data for two weed associations, both located in the Mediterranean and Irano-Turanian phytogeographical regions. The Scolymeto-Prosopidetum farcatae characterised fields in plains and intermountain valleys on deep *terra rossa*, basalt and calcareous soils (labelled "plains"). In contrast, the Ononis leiosperma-Carthus tenuis grew in fields with much shallower *terra rossa* and rendzina soils that were located on terraces and small patches in mountainous settings (labelled "hills")⁷². We recorded the weed flora of one arable field at Ramat Hanadiv in 2019 (Fig. 1b), where durum wheat was cultivated without the aid of pesticides or fertilisers. The grains are sown in December and not harvested in the following spring but eaten by local wildlife (mainly gazelle and boar). The remaining stubble is ploughed under with a tractor around October, which represents the only major anthropogenic disturbance.

Plant functional traits

To distinguish between arable and non-arable habitats we used the two functional traits flowering duration and vegetative regeneration. Both traits relate to the species' potential of rapid regeneration under conditions of high mechanical disturbance in arable environments^{29,30,35}.

Flowering duration is positively associated with conditions of high and unpredictable disturbance such as soil tillage¹⁵. Annuals and perennial species without extensive rhizomes that flower over extended periods begin to flower rapidly and simultaneously produce seeds, assuring reproduction in years when unpredictable disturbance events disrupt the life cycle early⁷³. In addition, the ability to produce multiple generations during a vegetation period adds to the success of long-flowering species in environments that are subjected to unpredictable disturbances. Flowering duration, measured as the maximum number of months a species flowers, therefore is a useful indicator for the conditions of mechanical disturbance in a given environment. However, as climatic factors influence flowering duration, this trait must be measured in the study area. As this is usually not possible in practice, we extracted flowering duration from the regional floras, *Flora Palaestina*⁷⁴ and *Flora of Turkey*⁷⁵. When archaeological weed seeds were only identified to the genus level but all regional species in this genus have a comparable flowering period, we used the average flowering period of all species.

The capacity of perennials to regenerate rapidly after mechanical disturbance events is associated with the presence of extensive root, rhizome, or stolon systems, and their ability to form new vegetative shoots from root or stem fragments^{42,76}. However, not all perennial species with rhizomes or stolons can rapidly regenerate after mechanical disturbance events. For example, *Urtica dioica* or *Phragmites australis* develop extensive clonal patches but are not well adapted to conditions of high disturbance¹⁵. Large terminal tubers and vertical tap roots can be classified as stationary sensu Håkansson⁴² and are equally sensitive to conditions of high disturbance. We classified species after their capacity to rapidly regenerate under conditions of high mechanical disturbance as *no/moderate capacity* (stationary perennials and perennials with extensive root or stem systems that are sensitive to disturbance) and *rapidly regenerating* (perennials that have extensive root or stem systems and rapidly regenerate from fragments). This classification is based on field observations and local floras^{74,75}.

Selection of archaeobotanical samples and weed taxa

To identify weed assemblages related to relevant crop-processing activities, a minimum of 100 cereal or pulse grains and 10 well preserved weed seeds were taken as cut-offs to include samples in the analysis. This numerical criterion was applied to all sites and excluded most samples with minor proportions of crop items that do likely not reflect processing activities and related weed assemblages (see Supplementary Table 3 for crop proportions per analysed samples). To enhance comparability between sites and samples, we excluded potential weed taxa that were likely dung-derived, collected, or not identified to a taxonomic level that allowed attributing a functional trait value. This selection process filtered all assemblages for taxa most likely related to cereal and pulse harvesting and processing.

Green³⁷ conducted the taphonomic analyses and selection of weed taxa for the samples from Çatalhöyük, Dja'de, and Jerf el Ahmar. All samples from Çatalhöyük represent storage contexts³⁶, whereas the samples from Dja'de and Jerf el Ahmar derive from primary contexts (hearths and floor layers) and secondary deposits (building collapse, midden deposits). The selected samples from Dja'de and Jerf el Ahmar were originally analysed by Willcox *et al.*¹ and Douché⁷⁷. The status of non-crop taxa as weed contaminants was confirmed via a crop processing analysis detailed in^{37,78}, indicating that the analysed samples from these sites represent crop processing by-products. Weed assemblages from processing by-products *can* be biased towards long-flowering species, while weeds in processing products may contain more short-flowering species⁷⁹. However, as all analysed samples represent by-products, such a bias can be ruled out for comparing conditions of disturbance at Çatalhöyük, Dja'de, and Jerf el Ahmar. Based on the crop-processing analysis, combined with the frequency and ecology of wild species in the assemblages, taxa that were likely gathered or represent ruderals were excluded for Çatalhöyük (*Descurainia sophia*, *Helianthemum* sp., *Teucrium* sp.), Dja'de (*Alyssum/Lepidium*, *Atriplex* sp., *Capparis* sp., *Hyoscyamus* sp., *Stipa* sp.), and Jerf el Ahmar (*Capparis* sp.) (for details see Green³⁷). Dung-derived taxa identified through previous taphonomic analyses were excluded from the samples of Çatalhöyük^{80,81}. Despite evidence for cattle manage-

ment and morphological changes at Dja'de⁸², dung burning as a significant factor in the formation of the earlier assemblages can be ruled out based on the rarity of small and hard-coated seeds that typically survive ruminant digestion^{37,83}.

The analysed samples from Atlit-Yam derived from a submerged well and we defined each layer from this well as one sample. Two layers that did not contain enough weed seeds were combined to one sample (210–230 cm and 230–150 cm)⁴⁴. No weed species were excluded from this dataset, as all remains were identified to the species level and represent obligatory or facultative arable weeds. For Netiv Hagdud, Kislev⁸⁴ summarised samples as per locus, which means that the samples we analysed represent loci and not individual archaeobotanical samples. We excluded all potential weeds that were not identified to the species or genus level, all rare taxa (present in only 1 locus), and the potential cultivars/target species (*Avena* spp., *Hordeum vulgare* subsp. *spontaneum*, *Triticum turgidum* subsp. *dicoccoides*, *Lathyrus* spp., *Lens* sp., *Vicia ervilia*).

The assemblage from Gilgal I derives from a single storage context dominated by wild barley and oat grains⁸⁵. The contaminants of the sample are most likely weeds harvested with the cereals, from which we excluded imprecise identifications (only Viciaeae), genus identifications where life history is unclear (*Alopecurus* sp.), and the potential cultivars/target species (*Avena sterilis*, *Hordeum vulgare* subsp. *spontaneum*, *Triticum turgidum* subsp. *dicoccoides*, *Lens* sp.).

The analysed assemblage from Ohalo II represents accumulations of plant remains on two consecutive floors of hut 1^{48,86}. These assemblages do not primarily represent crop processing products or by-products but accumulations of collected seeds and fruits. The inferred disturbance signatures do therefore represent an average from several vegetation units around Ohalo II, from where plant seeds and fruits were collected. We combined all taxa identified from both floors to one dataset, omitted the target species (*Avena sterilis*, *Hordeum vulgare* subsp. *spontaneum*, *Triticum turgidum* subsp. *dicoccoides*, *Lathyrus* sp., *Lens* sp., *Pisum* sp.) and analysed two selections of taxa from this assemblage: (1) a selection without taxa that were likely gathered for the construction of the hut

(*Atriplex leucoclada*, *A. rosea*, *Puccinellia* cf. *convoluta*, *Suaeda palaestina/fruticosa*)^{48,86}, and (2) the potential weed assemblage selected by Snir et al.⁴.

Data analysis

All analyses were performed using semi-quantitative datasets (presence/absence of species per sample), which has been shown to be as effective in distinguishing arable fields and different cultivation regimes as fully quantitative data^{43,87}. The floristic composition of individual sites and their relationship to each other was explored via correspondence analysis (CA) using CANOCO 5⁸⁸. Preparation of floristic datasets for CA, including standardising the taxonomy and determining frequency cut-offs for excluding rare species (we used 7% in the CA shown in Fig. 2), is detailed in Weide et al.²⁵. As sample distribution was potentially biased by the arch-effect, we detrended the ordination model by segments using a detrended correspondence analysis (DCA)⁸⁸. We used discriminant analysis to distinguish modern arable and non-arable habitats according to their disturbance conditions using IBM SPSS version 27. For this we determined an average score per functional trait for each sample (quadrat/relevé/plot) as follows:

$$\frac{\sum_i^n a_i k_i}{\sum_i^n k_i}$$

Where k_i equals 1 for semi-quantitative data, a_i = trait value for the i th species, and n = number of species recorded in each field. As k is always equal to 1 for semi-quantitative measures, the numerator is the sum of trait values for all species in the sample, while the denominator is the number of all species in the sample. The success of the discriminations was measured as the percentage of samples correctly reclassified as 'arable' or 'non-arable', using the discriminant function extracted from each analysis. The archaeobotanical samples were entered into the classification phase of the analyses as cases with unknown disturbance conditions. Each archaeobotanical sample was classified as

‘arable’ or ‘non-arable’ with a low (< 90%) or high (> 90 %) probability. All modern and archaeobotanical samples received a discriminant score, which we used to visualise the relative position of samples to each other by plotting the samples along the extracted discriminant function. Average attribute scores for each analysed modern and archaeobotanical sample, and the outputs of the discriminant analyses, are given in Supplementary Table 4.

Acknowledgements

We would like to thank Hagar Leschner, Neta Manela, Yoel Melamed, and Tamar Avin-Wittenberg for their great support in the preparation and realisation of the vegetation surveys that represent the basis of this study. We also thank Samuel Bowles and Greger Larson for valuable comments on previous drafts of this article. This research was supported by a Marie Skłodowska-Curie Individual Fellowship of the European Commission [grant number 838395].

Author Contributions

A.W. developed the original ideas and designed the study. A.W., J.G.H., J.W. and A.B. conducted field work and collected the plant functional trait data. G.D. and Y.O. contributed survey data and gave permission for their use. L.G., C.D. and M.T. provided archaeobotanical data and gave permission for their use. A.W. performed the data analysis and wrote the paper with the help of A.B. All authors were involved in the interpretation of the results and commented on the manuscript.

Competing Interests Statement

We have no competing interests.

Data Availability Statement

All data used to perform the discriminant analyses and their outputs are given in the supplementary materials. The modern floristic datasets and the archaeobotanical data analysed during the current study are not publicly available due to ongoing analyses of the samples and raw data. Upon completion of all analyses the raw datasets will be made publicly available. Parts of the modern floristic datasets are available from the corresponding author on reasonable request. The raw data on which the analyses from Çatalhöyük are based are fully published and publicly accessible in Green (2017).

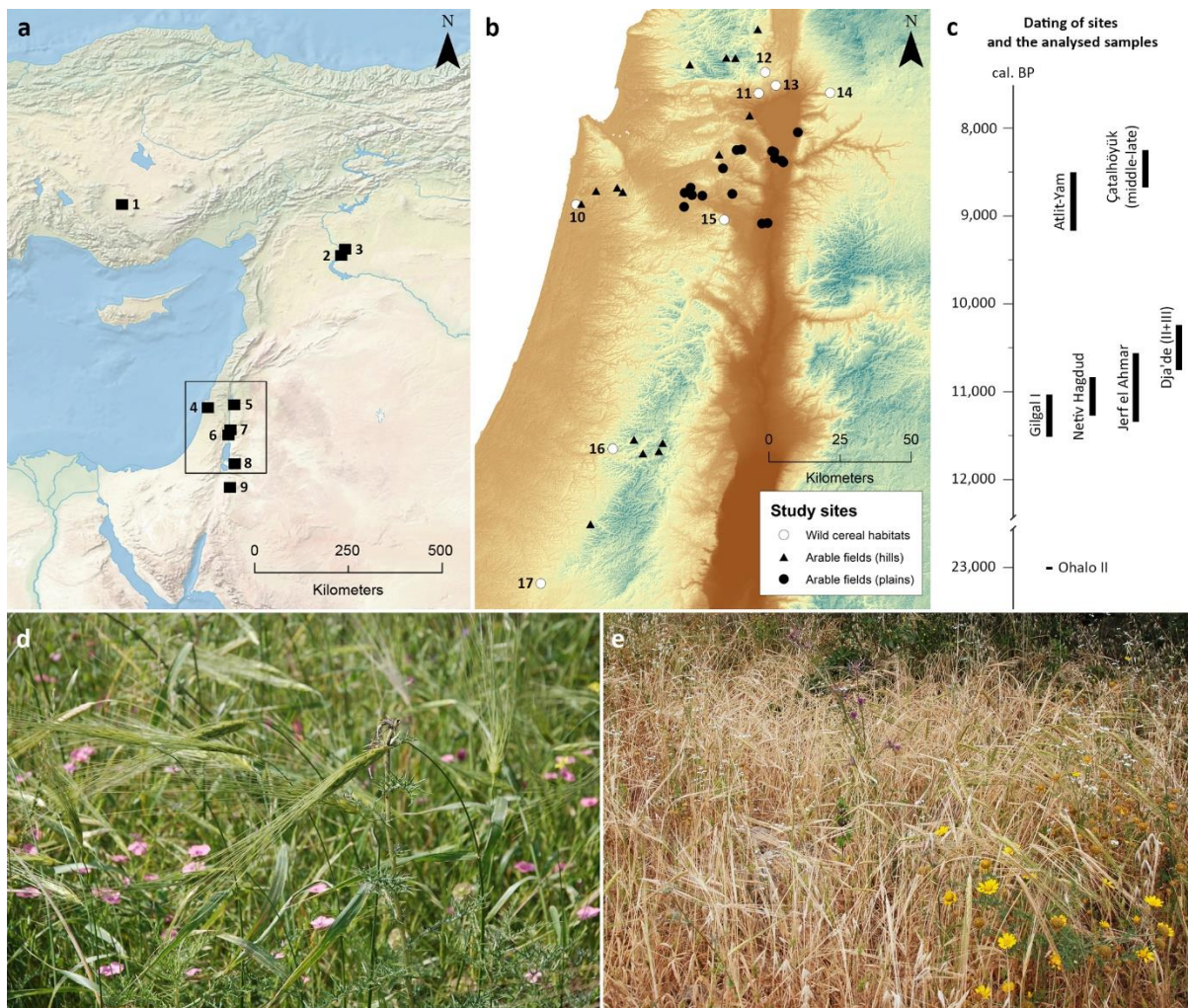


Fig. 1 a) Location of archaeological sites mentioned in the text; **b)** Location of arable fields and non-arable wild cereal habitats; **c)** Chronology of the archaeological sites and samples analysed in the study; note that Dja'de and Çatalhöyük were occupied for longer but not all phases are represented by the analysed samples; **d)** wild emmer wheat (*T. turgidum* subsp. *dicoccoides*) near the Sea of Galilee

578 lee, growing with facultative weeds like *Linum pubescens*; **e)** wild barley in the Upper Galilee, grow-
579 ing with facultative weeds like *Glebionis coronaria* and *Notobasis syriaca*. Key to archaeological sites:
580 1) Çatalhöyük, 2) Jerf el Ahmar, 3) Dja'de, 4) Atlit-Yam, 5) Ohalo II, 6) Netiv Hagdud, 7) Gilgal I, 8)
581 'Dhra, 9) Wadi Faynan 16; key to the surveyed wild cereal habitats: 10) Ramat Hanadiv, 11) Nahal
582 Amud, 12) Rosh Pina, 13) Karei Deshe, 14) Gamla, 15) Mt. Gilboa, 16) Kedoshim Forest, 17) Lehavim.
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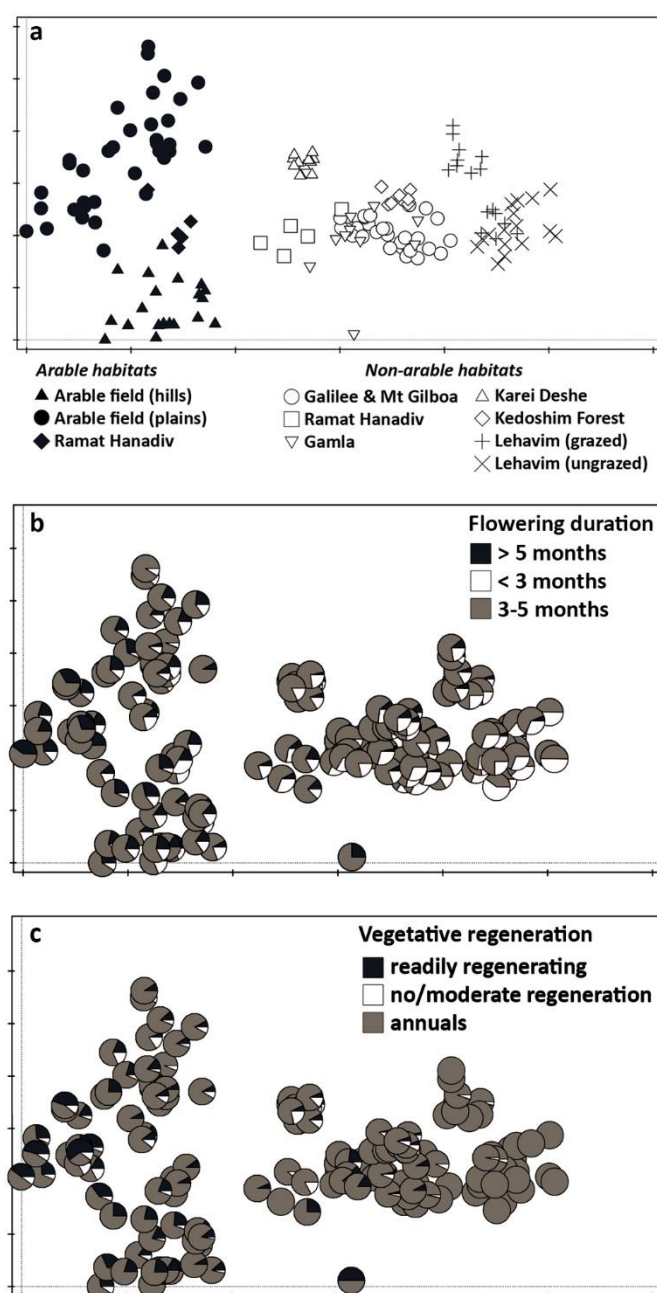


Fig. 2 a) DCA plot of samples from modern arable and non-arable habitats; **b)** distribution of long- and short-flowering species among the surveyed habitats; **c)** distribution of species after their capacity to regenerate vegetatively under conditions of high disturbance.

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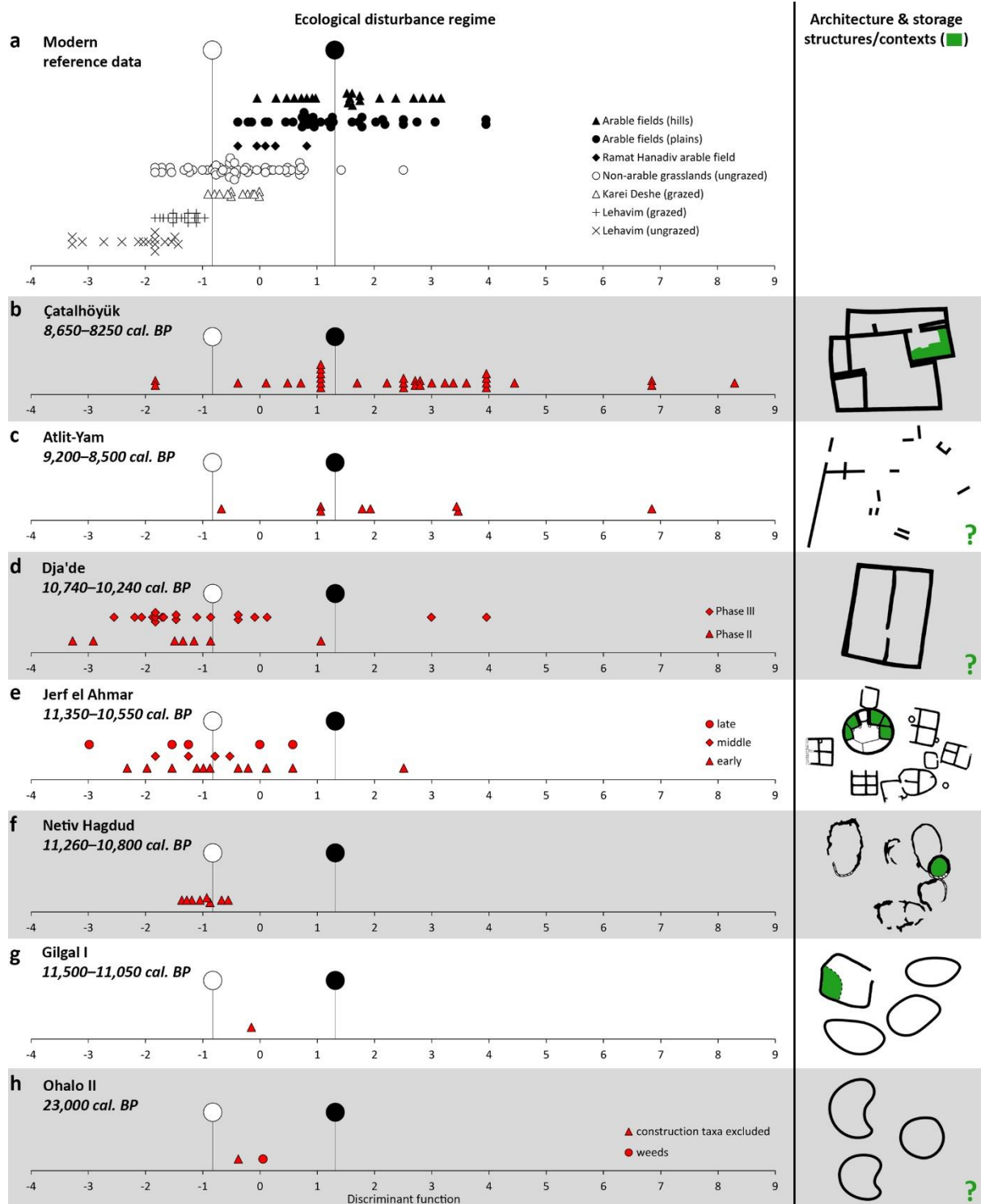


Fig. 3 Discriminant function extracted from the discriminant analysis using only flowering duration as a discriminating variable; the archaeobotanical samples (in red) are correlated with an example of the typical residential architecture (not to scale) of the analysed settlement phases and storage facilities (in green); **a**) modern reference data from arable (black symbols) and non-arable (open sym-

611 bols) habitats; 86.7% of all modern samples were correctly reclassified, larger symbols indicate
612 group centroids; **b)** samples from Çatalhöyük and building 52 (middle phase) with food storage bins
613 in a storage room, redrawn from Bogaard et al.⁴⁶; **c)** samples from Atlit-Yam and parts of the settle-
614 ment plan (storage mode unclear), redrawn from Galili et al.⁸⁹; **d)** samples from Dja'de with building
615 EA6 (phase II, storage mode unclear), redrawn from Douché⁵⁸; **e)** samples from Jerf el Ahmar with
616 architecture from level II/W (late phase) including the communal building EA30 with storage bins,
617 redrawn from Brenet et al.⁹⁰; **f)** samples from Netiv Hagdud and parts of the settlement plan with a
618 potential free-standing storage silo, redrawn from Bar-Yosef and Gopher⁶⁰; **g)** sample from Gilgal I
619 with parts of the settlement plan, the cereal hoard derives from structure 11, redrawn from Bar-
620 Yosef et al.⁹¹; **h)** samples from Ohalo II with parts of the settlement plan (arrangement of huts modi-
621 fied, storage mode unclear), redrawn from Weiss et al.⁴⁸.

622 **Table 1** Surveyed non-arable grasslands and dominant large-seeded grasses.

Site	Elevation (m a.s.l.)	MAP ^a (mm)	Soil	Potential vegetation ^b	Survey method ^c	Grazing	Large-seeded grasses				
							<i>Aegilops geniculata</i>	<i>Avena sterilis</i>	<i>Hordeum bulbosum</i>	<i>Hordeum vulgare</i> subsp. <i>spontaneum</i>	<i>Triticum turgidum</i> subsp. <i>dicoccoides</i>
Nahal Amud (north of Kahal)	130-140	671	terra rossa	Savannoid grassland	quadrats	none	X	X	X	X	X
Mt. Gilboa	415-425	398	terra rossa	Park forest	quadrats	none	X	X	X	X	X
Rosh Pina	480-490	632	terra rossa	Park forest	quadrats	none	X	X	X	X	
Gamla	420	568	grumosols	Park forest	quadrats	none		X	X		X
Ramat Hanadiv	110	585	terra rossa	Park forest	quadrats	none	X	X			
Karei Deshe	150	570	protogrumosols	Savannoid grassland	step-point	0.55 cows/ha	X ^d	X	X	X	X
Kedoshim Forest	400-500	550	terra rossa	Maquis and forests	nested plots	none	X	X	X	X	X
Lehavim	350-500	295	lithosol	Semi-steppe batha	quadrats	none flock of 600 sheep		X		X	
							large-seeded grasses rare due to heavy grazing				

623 ^a long-term mean annual precipitation of the nearest station, kindly provided by the Israel Meteorological Service; ^b after Danin⁶⁵; ^c see Methods for further details; ^d
624 here *Aegilops peregrina*

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Site (period)	Phase/assemblage (dates in cal. BP)	All sam- ples	DA 1 (using both functional traits)					DA 2 (only flowering duration)				
			Sample <i>n</i>	Non-arable		Arable		Sample <i>n</i>	Non-arable		Arable	
				<i>high prob*</i>	<i>low prob*</i>	<i>high prob</i>	<i>low prob</i>		<i>high prob</i>	<i>low prob</i>	<i>high prob</i>	<i>low prob</i>
Çatalhöyük (Late Neolithic)	8,650–8,250	33	21	1	1	18	1	33	2	2	21	8
	<i>Late (8,450–8,250)</i>	8	6			6		8			7	1
	<i>Middle (8,650–8,450)</i>	25	15	1	1	12	1	25	2	2	14	1
Atlit-Yam (PPNC)	9,200–8,500	8	2			1	1	8		1	5	2
Dja'de (early PPNB)	10,740–10,240	26	8	3	2	3		26	19	4	2	1
	<i>PPNB III (10,430–10,240)</i>	19	6	2	2	2		19	13	4	2	
	<i>PPNB II (10,740–10,430)</i>	7	2	1		1		7	6			1
Jerf el Ahmar (PPNA)	11,350–10,550	20	16	8	6		2	20	12	5	1	2
	<i>late (10,750–10,550)</i>	5	4	3			1	5	2	1	1	1
	<i>middle (11,260–10,860)</i>	4	4	2	2			4	3	1		
	<i>early (11,350–11,190)</i>	11	8	3	4		1	11	7	3		
Netiv Hagdud (PPNA)	11,260–10,800	8	8	8				8	6	2		
Gilgal I (PPNA)	11,500–11,050	1	1	1				1		1		
Ohalo II (Early Epipalaeolithic)	23,000	2	1		1			2		2		
	<i>without construction taxa</i>	1	1		1			1		1		
	<i>potential arable weeds</i>	1						1		1		

Table 2 Classification of archaeobotanical samples based on the discriminant functions extracted from both discriminant analyses.

* probability for correct classification of 0.9 (=90%) or higher; ** probability <0.9

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658 **Table 3** Centroid (C), variance (VAR), and standard deviation (SD) of
659 the archaeological datasets, based on the discriminant scores of the
660 archaeobotanical samples. DA1 = based on both traits; DA2 = based
661 on flowering duration only.

Site	DA 1				DA 2			
	<i>n</i>	<i>C</i>	<i>VAR</i>	<i>SD</i>	<i>n</i>	<i>C</i>	<i>VAR</i>	<i>SD</i>
Çatalhöyük	21	3.16	5.50	2.35	33	2.47	4.95	2.23
Atlit-Yam	2	-	-	-	8	2.36	5.08	2.25
Dja'de	8	-0.13	4.22	2.05	26	-1.01	2.64	1.63
Jerf el Ahmar	16	-0.90	0.34	0.85	20	-0.79	1.47	1.21
Netiv Hagdud	8	-1.44	0.05	0.21	8	-0.99	0.08	0.29

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