

The association of arable weeds with modern wild cereal habitats: implications for reconstructing the origins of plant cultivation in the Levant

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Abstract

Reconstructing the origins of plant cultivation in southwest Asia is crucial for understanding associated processes such as the emergence of sedentary communities and domesticated crops. Among the criteria archaeobotanists developed for identifying the earliest plant cultivation, the presence of potential arable weeds found in association with wild cereal and legume remains has been used as a basis for supporting models of prolonged wild plant cultivation before domesticated crops appear. However, the proposed weed floras mainly consist of genus-level identifications that do not differentiate between arable weeds and related species that characterise non-arable habitats. Here we test, for the first time, whether the potential arable weed taxa widely used to identify wild plant cultivation also occur in non-cultivated wild cereal populations. Based on modern survey data from the southern Levant we show that the proposed weed taxa characterise both grasslands and fields. Our findings, therefore, do not support the use of these taxa for reconstructing early cultivation. Instead, for future studies we suggest an approach based on the analysis of plant functional traits related to major agroecological variables such as fertility and disturbance, which has the potential to overcome some of the methodological problems.

Keywords

Origins of agriculture, cultivation, arable weeds, wild cereals, Pre-Pottery Neolithic, southwest Asia

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Introduction

The Pre-Pottery Neolithic (PPN) is characterised by the development of sedentary farming societies throughout the Levant encompassing parts of modern Jordan, Israel, Palestine, Syria and southeast Anatolia (Kuijt and Goring-Morris 2002; Byrd 2005). During the earlier phase of the PPN (PPNA: ca. 12,000-10,700 cal. BP), charred remains of the wild progenitors of the cereal founder crops einkorn (*Triticum monococcum* subsp. *aegilopoides*), emmer (*Triticum turgidum* subsp. *dicoccoides*) and barley (*Hordeum vulgare* subsp. *spontaneum*) dominate charred botanical assemblages (van Zeist and Bakker-Heeres 1984; Kislev 1997; Colledge 2001; Weiss et al. 2006; Willcox et al. 2008; Weiss and Zohary 2011; White and Makarewicz 2012; Colledge et al. 2018). The later phase (PPNB: ca. 10,700-9,000/8,500 cal. BP) provides widespread evidence for cereal domestication, which is primarily based on morphological traits indicative for the development of non-shattering ears (Nesbitt 2002; Tanno and Willcox 2006; Tanno and Willcox 2012; Arranz-Otaegui et al. 2016). Most researchers agree that morphological domestication traits related to crop reproduction in farming regimes can only be selected for after plants were taken into cultivation, which is why these traits are interpreted as unequivocal evidence for the beginnings of farming (Hillman and Davies 1990; Nesbitt 2002; Gepts 2004; Fuller and Allaby 2009). However, it is still under debate when cereal cultivation began and whether PPNA groups primarily gathered wild cereals or already cultivated them on a regular basis (Snir et al. 2015; Abbo and Gopher 2017; Asouti 2017).

In order to approach this question, archaeobotanists have developed various criteria to identify early cereal cultivation in the absence of reliable domestication markers (Supplementary Table 1). These primarily include the finding of substantial amounts of stored cereal remains (Weiss et al. 2006; Kislev et al. 2010) and/or storage structures (Kuijt and Finlayson 2009; Willcox and Stordeur 2012), large 'cultivated-type' cereal grains (Hopf 1983; Hillman et al. 2001; Meadows 2004; Willcox 2004; White and Makarewicz 2012; Colledge et al. 2018), and the presence of potential arable weed floras (Colledge 1998; Willcox et al. 2008; White and Makarewicz 2012; Willcox 2012; Snir et al. 2015; Colledge et al. 2018). In addition to the wild progenitors of the cereal founder crops, the proposed cultivars include wild oat (*Avena sterilis*), two-grained forms of wild einkorn and/or rye (*Secale* sp.) and occasionally associated legumes. However, the above-mentioned cultivation indicators have also been criticised as ambiguous arguments, because they do not fully rule out large-scale gathering of wild cereals from dense stands in grassland habitats. First, grain storage in dedicated storage structures is not limited to cultivated seeds as seasonally abundant wild resources can be collected and stored as well (Testart 1982; Harlan 1989). Second, wild cereal grain size is influenced by a variety of climatic and edaphic factors, which are not necessarily related to human management practices. The argument that increased grain sizes indicate cultivation is mostly based on the expectation that grains sown on tilled soils experience enhanced growing conditions and are buried deeper, which can select for larger seeds that produce larger, more competitive seedlings (Harlan et al. 1973; Willcox 2004). However, changing environmental and climatic conditions during the Early Holocene, including a strong inter-specific competition in grassland habitats and increased productivity, could also have affected cereal grain size fluctuations over time (Blumler 2002; Asouti 2017). Additional uncertainties relate to the effect of different charring conditions on cereal grain size and shape (Braadbaart and Bergen 2005; Charles et al. 2015), which were not systematically distinguished from a true size increase in the analysed assemblages. The amount of recovered grains, potential food storage structures and large grain dimensions are therefore ambiguous arguments to distinguish between gathering and

cultivation reliably, which is why most archaeobotanists focus on the identification of potential arable weeds.

One of the earliest systematic attempts to identify an arable weed flora associated with wild cereals is the multivariate analysis of the archaeobotanical assemblage from Mureybet in the upper Euphrates basin in Syria by S. Colledge (Colledge 1998). She coded the floristic composition of the analysed samples according to vegetation units associated with different disturbance regimes and found that species typical for arable environments and annuals from batha (=garigue) communities characterise PPNA and PPNB samples as opposed to those from the late Epipalaeolithic. She suggested that these changes reflect accelerated disturbances of the vegetation from where wild cereals were harvested, which she attributed to soil tillage indicative of 'pre-domestication cultivation'. A comparable approach – using taxa known to include common arable weeds as cultivation indicators – was simultaneously adopted by G. Willcox. He identified a set of potential arable weed taxa at several PPNA and early PPNB sites in northern Syria and argued that they were part of local weed floras, which represents his main argument among several other lines of evidence for local wild plant cultivation (Willcox 1996; Willcox et al. 2008; Willcox 2012). His two main criteria for including taxa in this list were their occurrence in weed assemblages from later farming sites and the absence of ethnobotanical information on the utility of their fruits or seeds. Willcox excluded species with edible seeds that were likely gathered and showed that the number of potential weed taxa in some PPNA assemblages is comparable to that of PPNB farming contexts. However, Willcox's taxa mostly include genera and almost no species identifications. To justify the usefulness of these genera as cultivation indicators, he listed extant weed species for each genus that were recorded during weed surveys in Palestine during the early 20th century (Zohary 1950).

Today this selection of potential arable weed taxa – or the interpretation of seeds as potential weeds in general – is widely accepted among archaeobotanists for identifying the cultivation of primarily wild cereals in the Levant and adjacent regions (White and Makarewicz 2012; Riehl et al. 2013; Snir et al. 2015; Arranz-Otaegui et al. 2016; Colledge et al. 2018; Fuller and Stevens 2018). However, authors have also included edible grasses such as *Aegilops* spp., *Avena* spp., *Hordeum* spp. or *Phalaris* spp. into their potential weed floras, which could also have been gathered as food sources (Weide et al. 2018). These extended weed lists may therefore be less indicative of cultivation practices, which is why in the present study we focus on the taxa compiled by Willcox (2012).

An obvious problem with a list of genera indicating cultivation practices is that most of the taxa include facultative weed species which also grow alongside wild cereals in Levantine grasslands (Zohary 1950; Hillman et al. 1989; Abbo et al. 2012). This indicates that many arable weeds originated from these grasslands (Zohary 1950; Weide et al. 2018), which further complicates the identification of cultivation activities based on a coarse taxonomic approach and also explains why taxa abundant in foraging contexts may represent successful weeds at farming sites. Theoretically, the regular harvesting of wild cereals from non-cultivated habitats should result in the incorporation of some of these taxa in wild cereal harvests, especially when they were reaped with sickles like the earliest domesticated cereals (Maeda et al. 2016). The potential weed floras could then be indicative of the intensive exploitation of wild cereal stands, resulting in the accumulation of seeds from weed relatives in archaeobotanical assemblages (see also Supplementary text 1). Despite these uncertainties, the pre-domestication cultivation hypothesis assumes that the compiled set of genera characterised arable habitats and it was never systematically tested whether these taxa could likewise derive from non-arable grasslands.

Traditional agriculture and associated weed floras in Mandatory Palestine

A further issue relates to the use of modern weed floras as analogies for the species that colonised the earliest cultivated fields in the Levant. It is well established that different environmental conditions and crop husbandry practices shape the weed communities that develop in cultivated fields (Ellenberg 1950; Zohary 1950; Jones 1992). Therefore, when we use modern weed surveys as a comparative dataset for interpreting prehistoric seed assemblages, we must account for the environmental and historical context in which the data were collected. The weed accounts Willcox (2012) used for partly justifying his selection of potential weed taxa were recorded by M. Zohary in Mandatory Palestine during the first half of the 20th century (Zohary 1950) (Fig. 1). Zohary divided the recorded weed floras into several associations, of which each was characteristic for a particular environmental setting and began to disappear with the mechanisation of agricultural practices. He provided 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. 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 (Dan et al. 1970).

Zohary provided limited information on the husbandry regimes associated with the surveyed fields, but his remarks on the cultivated crops, fallow periods and absence of mechanised tillage in the hills suggest that the fields were still managed as part of the traditional *musha'a* system. The *musha'a* was a communal land tenure system distributed from Upper Egypt across the Levant into parts of Iraq until the early 20th century (El-Eini 2006). Rotation between winter and summer crops with regular fallow periods characterised the associated crop husbandry regimes. During the survey period in Mandatory Palestine, the two-field system was still common with a winter cereal or legume on one field and a summer crop of sesame or Indian millet on the second after it remained fallow during the rainy period (Zohary 1950; Atran 1986). The ard, or scratch-plough, was used to till the soils with the help of draught animals (Palmer 1998b). Fields were rarely irrigated and only received manure when livestock grazed on the fields after the harvests.

The traditional agricultural practices associated with the *musha'a* mostly vanished from the region, but C. Palmer was able to investigate comparable husbandry regimes and associated weed floras in northern Jordan during the 1990s (Palmer 1994; Palmer 1998a; Palmer 1998b). Like Zohary she divided the study region into hills and plains where husbandry regimes differed according to the local topography and soil conditions. Tractor ploughing and 3-year crop rotation cycles were more common in the plains whereas animal tillage using an ard and biennial crop rotations were practised on the shallow and stony soils in the hills (Palmer 1998b). The weed floras she identified in both regions were comparable to those described by Zohary, which indicates that the environmental setting primarily determined the floristic composition of the weed associations. However, Palmer (1998a) suggested that the different regional crop-rotation regimes also caused some of the floristic variation. In applying FIBS (functional interpretation of botanical surveys) to the same datasets, Bogaard et al. (1999) successfully related plant functional attributes indicative of species' potential in relation to soil fertility and disturbance to growing conditions under the different rotation regimes. According to their study, attributes related to high productivity characterise weeds associated with legume crops in the two and three-year rotation regimes, indicating that legume cultivation maintains a higher soil fertility than a fallow-cereal rotation. The integration of a cultivated fallow (no crops but repeatedly tilled during the year) favoured species adapted to survive frequent disturbance events. Demonstrably,

therefore, the floristic composition of East Mediterranean weed associations is also influenced by different crop-rotation regimes and not only by local environmental conditions.

The impact of these factors on the composition of weed floras recorded by Zohary remains somewhat unclear due to the lack of detailed information on the associated husbandry regimes. Zohary (1950) mentioned unmechanised tilling and biennial crop-rotation for the hilly region, but did not describe husbandry regimes in the plains. An analysis of the weed records according to functional attributes that are related to different crop-rotation regimes has the potential to identify husbandry-related differences among the weed floras but would exceed the scope of the present study. However, regarding archaeological applications it is important to recognise that Zohary's weed associations characterise specific crop husbandry regimes in distinct environmental settings of Mandatory Palestine, which may significantly differ from prehistoric cultural and environmental contexts.

Aims of study

In this study we test, for the first time, whether the potential arable weed taxa widely used in archaeobotany to identify pre-domestication cultivation also occur in non-cultivated grasslands that support dense wild cereal populations. In order to test this hypothesis, we surveyed five grassland habitats in northern Israel dominated by wild barley (*Hordeum vulgare* subsp. *spontaneum*), wild emmer (*Triticum turgidum* subsp. *dicoccoides*) and/or wild oat (*Avena sterilis*). Some surveyed habitats contained dense populations of goatgrasses (*Aegilops* spp.) and bulbous barley (*Hordeum bulbosum*), two taxa that occur in PPNA plant assemblages alongside the wild crop progenitors. Moreover, the study region is of major importance for the pre-domestication cultivation hypothesis, because it contains several Epipalaeolithic and PPNA sites for which wild cereal cultivation was proposed (see Supplementary Table 1). We then compared the floristic composition of these wild cereal communities to three additional datasets from local wild cereal communities and to the arable weed floras recorded by M. Zohary during the early 20th century (Zohary 1950). Willcox (2012) used Zohary's survey data to compile extant weed species for his set of potential weed genera, so we directly contrast the composition of grassland communities to the weed associations that partly justify the pre-domestication cultivation hypothesis. We test how accurately floristic composition separates modern arable fields and non-arable grasslands and analyse the occurrence and frequency distribution of weed species among both habitats with a focus on the potential arable weed taxa.

Materials and methods

Study sites and field methods

We surveyed the herbaceous vegetation at five sites in the Mediterranean and Irano-Turanian phyto-geographical regions (Zohary 1973; Danin 1988) of northern Israel in late April, 2019 (Fig. 1). All sites 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 two criteria: the presence and dominance of at least one large-seeded grass species (Fig. 2) and the recent land-use history. None of the surveyed habitats had been cultivated during the last ca. 50 years; nor were they exposed to high levels of grazing, which would have resulted in the disappearance of dense wild cereal stands. The only population that had significant shade from tree cover (ca. 70 %) was surveyed in a *Pinus halepensis* grove at Rosh Pina (ROS-02). The surveyed plots at Ramat Hanadiv, Mount Gilboa, Nahal Amud and

Rosh Pina are located on *terra rossa* soil over dolomite or limestone, whereas the study site at Gamla lies in an area with protogrumosols and grumosols over basalt.

At each site we surveyed the vegetation in two plots following the method described by Jones et al. (1999) and adjusted by Bogaard et al. (2018). 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 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. At Ramat Hanadiv, the two surveyed transects were both located in former *Cupressus sempervirens* groves, which have been cleared between 2003-2005 (pers. comm. Liat Hadar). One transect (KEB-01) represents an area re-colonised by local grassland species, while the second transect (KEB-02) recorded the weed flora of a durum wheat field 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.

Additional datasets

We used previously recorded datasets to compare the floristic composition of the surveyed grasslands to local arable weed floras and other wild cereal habitats (Fig. 1). Comparative data for arable fields were extracted from Zohary (1950), who recorded relevés covering a total of 100m² per field in Mandatory Palestine.

To expand the floristic dataset for wild cereal habitats we analysed vegetation survey data from selected plots of three additional sites. The Karei Deshe Experimental Farm is located north of the Sea of Galilee near Chorazim. These Mediterranean grasslands receive ca. 570 mm of annual rainfall and grow on brown basaltic protogrumosols (Dan et al. 1970). We selected survey data from two plots of 31.1 and 28.2 ha, which were sampled each year between 2014-2019 and have 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 method (Sternberg et al. 2000). It has been acknowledged that this method can underestimate species richness (Sternberg et al. 2015). However, as we describe below, for the statistical analyses we excluded rare species from all datasets.

The second additional dataset representative of a wild cereal habitat derives from cleared plots in a *Pinus halepensis* plantation at the long-term ecological research (LTER) site of Kedoshim Forest in the Jerusalem Mountains. The site receives ca. 550 mm annual rainfall and is situated in the Mediterranean phytogeographical region on hard dolomite and lime with shallow *terra rossa* soils (Calev et al. 2016). 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 1m*1m.

The site of Lehavim in the Goral Hills, northern Negev, is located in the Irano-Turanian phytogeographical region and represents the driest research site in this study with ca. 295 mm annual precipitation (Osem et al. 2002; Dovrat et al. 2020). The loamy soils are of a brown desert skeletal type and developed on limestone, dolomite and chalk. The selected dataset derives from four 10*10 m plots located on the wadi margins, which were protected from grazing during the entire survey period between

1996-1999. Every year, all species were recorded in four to five 20*20 cm quadrats per plot. The last year received only 40 mm rainfall and was the driest locally recorded year between 1951 and 1999 (Osem et al. 2002).

Data preparation and analysis

To compare datasets collected with different survey methods (relevé method, step-point method and quadrat sampling) and by different teams, taxonomy was updated using Euro+Med PlantBase (Euro+Med 2020). All analyses were conducted semi-quantitatively (presence/absence of species per transect/relevé/plot). The floristic composition of individual sites and their relationship to each other was explored via correspondence analyses (CA) using CANOCO 5 (Šmilauer and Lepš 2014) (see Supplementary text 2 for procedure to exclude rare species). Crops, target species (see Tab. 1) and large woody perennials (trees and large shrubs) were removed from all datasets to explore variation and potential differences based on the herbaceous vegetation alone. In case sample distribution was potentially biased by the arch-effect, we detrended the ordination model by segments using a detrended correspondence analysis (DCA) (Šmilauer and Lepš 2014). When detrending did not successfully reduce the arch-effect, we used a normal CA.

Results

Floristic variation within wild cereal habitats and arable fields

Based on the wild cereal habitats recorded during the 2019 surveys and the arable fields surveyed by M. Zohary, species richness is higher in wild cereal communities (210 species, mean $[M] = 59.1$ per transect, 9 transects; Tab. 2) than in cultivated fields (149 species, $M = 23.6$ per field, 57 fields). The proportion of annuals among all wild cereal stands ($M = 89.2\%$) and arable fields ($M = 85.2\%$) is comparable.

A DCA of the dataset recorded in 2019 based on all 50 quadrats and 75 species (5% frequency cut-off) separated the durum wheat field at Ramat Hanadiv (Keb-02) from the wild cereal stands along the first axis (Fig. 3). This axis also ordered the wild cereal habitats according to their relative geographic location and distance from the Mediterranean coast. The cleared cypress grove re-colonised by local grassland vegetation at Ramat Hanadiv (KEB-01) plots closest to the arable field at the same site, while most samples from habitats that are ca. 50-60 km inland in the Upper and Lower Galilee (AMU-01/02, ROS-01) and at Mt. Gilboa (GIL-01/02) form a distinct group. Gamla, ca. 25 km further inland, plots at the positive end of the first axis and the ordination diagram does not separate quadrats dominated by wild emmer (GAM-01) or *Avena sterilis* (GAM-02). The pine grove at Rosh Pina (ROS-02) represents an outlier towards the lower end of the second axis. These effects of geographic location on the observed variation may be due to differences in soils (Gamla is the only site located on protogrumosols/grumosols) and vegetation types (the pine grove at ROS-02 has the smallest number of species), but not precipitation (sites in the Galilee and at Mt. Gilboa cluster but have the highest and lowest mean annual precipitation, respectively).

A CA based on the 56 arable fields recorded by M. Zohary and 80 species (10 % frequency cut-off) separated the lowland fields (plains) from upland locations (hills) according to their phytosociological weed associations along the first axis (Fig. 4a). Factors that cause the observed variation likely include regional soil conditions (Fig. 4b), although different tillage methods dictated by the topographic

settings may have contributed to the distinct weed floras (Zohary 1950; Palmer 1998a; Bogaard et al. 1999). Fields in plains show considerably more variation along the second axis than fields in hills, which seems to be caused by differing edaphic conditions but also a steep precipitation gradient. Fields trending towards the positive end of axis 2, located in the Esraelon Plain and Lower Galilee, belong to the Mediterranean temperate zone (long-term mean of ca. 400-600 mm annual rainfall between 1961-1990) with *terra rossa* and basalt soils. In contrast, fields trending towards the negative end of axis 2 are located along the southern shore of the Sea of Galilee, in the Jordan Valley and Beth-Shean Valley and received only about 300-400 mm mean annual rainfall (1961-1990) on calcareous soils that formed over chalky and marly sediments of Lake Lisan (Dan et al. 1970; Danin and Orshan 1999) (Fig. 4b). The proximity to the water sources of the Sea of Galilee and Jordan River allowed the irrigation of some fields in this semi-arid climatic zone. The irrigated fields do not cluster separately, but we cannot rule out that we lack information about the irrigation of the other fields in this region. Weed floras recorded from fallow fields plot with all three groups and do not seem to drive the observed patterns (Fig. 4b). Likewise, coding the fields after crop species indicates that the cultivation of different cereals or legumes, as far as this is known, did not cause the main variation within or between the weed associations (Fig. 4c).

Separation of wild cereal habitats and arable fields based on their floristic composition

A DCA based on 106 samples (quadrats/relevés) from wild cereal stands and arable fields with 114 species (7 % frequency cut-off) separated all non-cultivated grassland habitats from fields along the first axis, while the second axis accounts for most of the variability within these groups (Fig. 5). The two transects from Ramat Hanadiv, representative of cypress groves cleared ca. 15 years ago, plot in a central position between the fields and non-cultivated grasslands. The re-colonised transect (KEB-01) is positioned near the other wild cereal stands, while the durum wheat field (KEB-02) trends towards fields in mountainous areas (Fig. 5).

In order to test whether or not the observed separation between grassland habitats and arable fields is biased by methodological issues such as the distinct survey methods, we integrated independently collected data from three additional wild cereal habitats into our dataset (see Supplementary Text 3 and Supplementary Figures 1-2 for an individual exploration of the additional sites). In a DCA with 102 samples (transects/relevés/plots) from all sites and 154 species (9 % frequency cut-off), the three additional sites plot with the other wild cereal stands and confirm their separation from arable fields along the first axis (Fig. 6). Transects from Karei Deshe and Nahal Amud do not overlap, although these sites are only 6 km apart. The cleared pine plantation at Kedoshim Forest plots closest to Rosh Pina and Mt. Gilboa, whereas samples from Lehavim in the northern Negev, the most arid site in the dataset, form a separate cluster.

The occurrence of arable weeds in fields and grasslands

The occurrence of arable weeds, and potential weed taxa as defined by Willcox (2012), was analysed based on all fields and transects in wild cereal stands including the three additional sites. One plot at Kedoshim Forest did not contain wild cereals and was omitted from the analyses, which reduced the dataset to 423 species in 57 fields and 43 transects/plots in grasslands. Figure 7 shows the distribution of species among arable fields and wild cereal stands with a separate quantification for the species that belong to one of the potential arable weed taxa. Considering the complete dataset, the number

of species only occurring in fields or in fields and grasslands is comparable, while most species only occur in grasslands. Among species belonging to one of the potential weed taxa, species occurring in fields and wild cereal stands are less common as opposed to species recorded only in fields or grasslands (Fig. 7; Tab. 3). The proportion of recorded species which solely occur in fields is higher within the selection of potential weed genera (39 %) as opposed to all recorded species (17 %). This means that Willcox' list of potential weed taxa excludes many genera which, according to our dataset, would not be indicative of arable environments. Supplementary Table 2 lists species with their frequencies that occur together in arable fields and grasslands or only in arable fields.

Figure 8 shows the occurrence of potential arable weed taxa among arable fields and grasslands, based on the DCA with all sites and 154 species (9 % frequency cut-off, see Fig. 6). As illustrated by the pie charts, species belonging to the potential weed taxa are not confined to arable fields but also occur among the non-cultivated grasslands. Figure 9 compares the frequency of species belonging to the potential weed taxa among the analysed samples from both habitats. This set of species, with a 5 % frequency cut-off, shows a symmetric, unimodal frequency distribution among arable habitats, but a right skewed distribution among wild cereal stands with a higher maximum number of taxa per sample (Fig. 10). However, samples without any of the potential arable weed taxa were more common among wild cereal stands than among arable fields. We found five species belonging to potential weed taxa among the wild cereal habitats that had previously been considered obligatory weeds (Zohary 1950; Willcox 2012) (Tab. 3).

Discussion and conclusions

Our results show that arable fields and grassland habitats dominated by wild cereals can be clearly separated based on species composition. This separation is independent of the survey methods applied and the climatic and environmental zones in which the fields or grassland habitats were located. Regional topographic and edaphic differences cause the main variation among the fields, which may partly be related to their effect on the choice of local husbandry methods (Palmer 1998a; Bogaard et al. 1999). In contrast, variation in grassland composition is primarily related to different soils and precipitation regimes (Danin 1988; Danin and Orshan 1990; Golodets et al. 2013; Dovrat et al. 2020), as grazing did not play a large role in shaping the sampled communities. They are all dominated by tall, annual grasses, which would decline under higher stocking rates (Noy-Meir et al. 1989; Noy-Meir 1990; Sternberg et al. 2015).

It might have been expected that grassland communities in the study area comprise floristic remnants from former land-use and cultivation activities, which would blur their separation from cultivated fields. However, this seems not to be the case and the surveyed wild cereal communities, although located on relatively small patches within an intensively cultivated landscape, are remarkably different from local weed floras which developed under traditional agricultural practices. Moreover, the fact that the durum wheat field and the re-colonised grassland at Ramat Hanadiv, both situated in former cypress groves cleared ca. 15 years ago, each trend towards the fields and wild cereal habitats in the ordination diagram, respectively, further emphasises the utility of floristic (species-level) variation to identify arable environments. These patterns indicate that components of former vegetation communities soon disappear when environmental factors or human land-use practices change.

Such consistent differences in species composition between arable fields and non-arable grasslands are a product of small-scale differences in the expression of key ecosystem processes in the two contrasted vegetation types that favour different annual plant communities. First, both habitats are

fertile, or include fertile microhabitats. This allows the rapid vegetative growth necessary for short-lived, annual species (Grime 2001; Wright et al. 2004). Secondly, both are subject to disturbance, which partially or completely destroys plant biomass. This facilitates colonisation by annual species and in the most severely disturbed habitats, miniaturisation enables annuals to complete their life cycle rapidly (Grime 2001; Hodgson et al. 2020). In semi-arid Mediterranean grassland, the main disturbance events relate to grazing, summer drought and wildfires (Grime 2001), while in arable habitats disturbances include ploughing, weeding and harvesting (Jones et al. 2000; Bogaard et al. 2001). These markedly different disturbance regimes have selected for contrasting ecological specialisations and generated distinctive vegetation communities. As a result, the arable habitat has no exact non-arable equivalent. Thus, when cultivated land is abandoned – even though arable weed species will initially predominate in the soil seed bank – or forests are cleared, the vegetation is expected to be colonised primarily by (better-adapted) non-arable species. The floristic composition of a modern wild cereal community should therefore be treated as a function of current ecosystem processes but not as a consequence of past cultivation activities.

We must emphasise that we found several species among the surveyed wild cereal habitats which Willcox (2012) listed as obligatory weeds (Tab. 3). This designation was based on Zohary (1950), who did not yet record these species outside of cultivated areas. Today it is well established that these species do occur in non-cultivated areas, which is partly due to conservation efforts and the establishment of protected habitats (Danin and Orshan 1999). The use of ‘obligatory weeds’ as definite cultivation indicators should therefore be treated with caution and their absence outside of cultivation may well be based on the prevailing land-use practices.

Our main question focused on the utility of the set of potential arable weed taxa as defined by Willcox (2012) and widely used to reconstruct early plant cultivation in the Levant and adjacent regions. Although fields and grasslands could be reliably separated based on their floristic composition, species that belong to the potential arable weed taxa are equally distributed among both groups. Not only do the potential weed species have comparable frequencies among the studied wild cereal habitats and arable fields, but their number per site can be *higher* in wild cereal communities, which is likely due to the greater species richness in non-arable grasslands. However, application of these quantitative patterns to archaeobotanical samples as a means of identifying cultivation is questionable, because for most archaeological contexts we must expect that plant remains in one sample represent harvests from multiple fields (large storage facilities) or even the accumulation of weed seeds from several years (midden deposits). The abundance of potential weed taxa in archaeological deposits is strongly related to these taphonomic factors, which mask their original abundance in fields or grasslands. The relatively high numbers of potential weeds in early Neolithic assemblages, ranging between 10-20 taxa per site (Willcox 2012), likely reflect such processes.

Based on the results of this study we cannot support the use of a selective set of potential arable weed taxa to identify early plant cultivation reliably. They mostly include whole genera and seem to characterise fields and wild cereal stands equally in the study region. On the other hand, our data show that species composition of arable environments *can* be distinguished reliably from that of non-arable grasslands. The main problem therefore seems to be the selective use of whole genera as indicators for cultivation activities. Moreover, the composition of the selected weed taxa is strongly associated with the environmental and cultural context in which the recorded associations developed. We have no reason to believe that the traditional Mediterranean crop-husbandry methods are directly comparable to prehistoric contexts (cf. Halstead 1987), which is why we must generally question taxonomic

approaches for identifying Early Holocene wild cereal cultivation based on modern arable weed surveys.

The present study also has limitations that need to be addressed. We analysed data from a limited study region, which represent local floristic patterns and cannot be used to address taxonomic differences between arable and non-arable habitats elsewhere. Some of the species we listed as occurring only in arable fields or grasslands (e.g. in Fig. 9) can occur in other habitats outside of the study region, which is why these specific floristic analyses are only representative for the surveyed communities. However, despite the fact that we have only analysed data from a limited geographical area, we could already show that 12 out of 20 potential weed genera are not solely indicative of arable habitats. We must therefore expect that the distinction between taxa indicative for arable or non-arable environments becomes even more blurred when larger datasets from a wider region are taken into account. This further emphasises the problems with a *taxonomic* approach and the use of specific taxa – often whole genera – to identify the beginnings of cultivation. Although it may be possible to isolate some obligatory weed species indicative of modern arable environments by using a larger dataset, their applicability to Early Holocene datasets would still be questionable for the reasons explained above. Our most important finding regarding the identification of cultivation activities based on potential weed seeds is that the distinct composition of species in arable environments and non-arable grasslands is primarily based on current ecological processes, and changes rapidly with a shift in land-use practices. This principle can be applied to archaeobotanical datasets by analysing potential weed assemblages according to the ecological adaptations of constituent species. This can be realised in future studies via the analysis of functional traits indicative of the species' potential in relation to major agroecological variables such as fertility and disturbance (Charles et al. 1997; Bogaard et al. 1999; Jones et al. 1999; Jones et al. 2000; Charles et al. 2003). A functional trait analysis can provide direct insights into the ecological conditions under which the respective seed assemblages formed, and whether or not these conditions include factors characteristic for arable environments. Moreover, functional ecology has the great advantage that it is applicable to assemblages from different regions and chronological contexts (Bogaard 2004; Bogaard et al. 2016; Bogaard et al. 2018). This makes it a promising candidate for overcoming some of the problems related to current approaches for identifying the beginnings of plant cultivation in the Levant and other regions of southwest Asia.

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Declaration of interest statement

No potential conflict of interest was reported by the authors.

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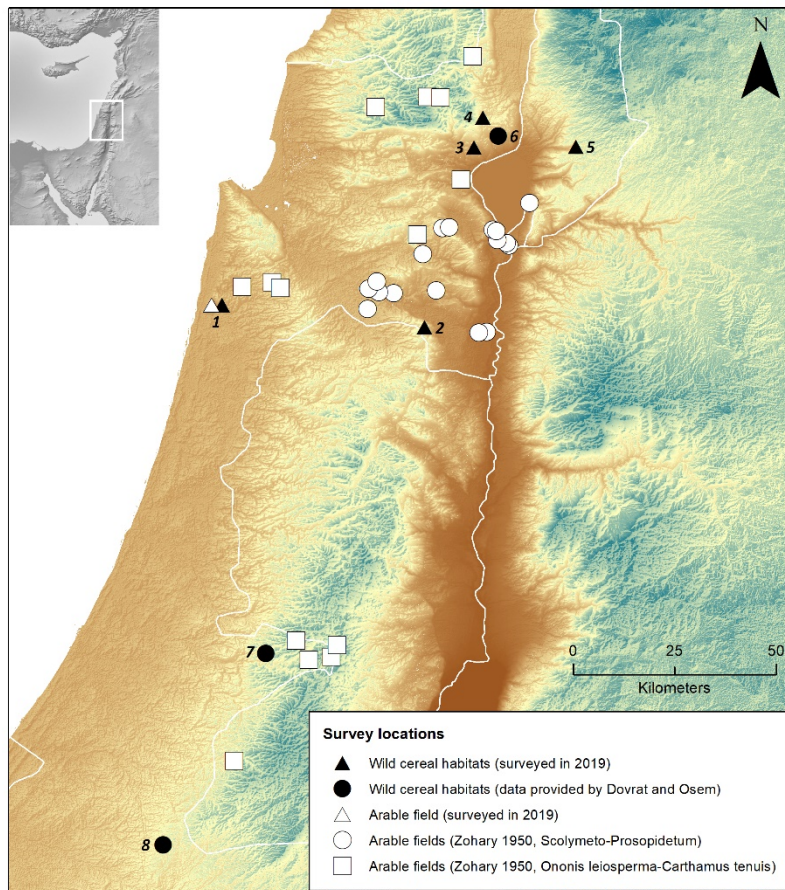


Fig. 1 Locations of the surveyed sites analysed in this study. We reconstructed the position of the fields based on Zohary's site descriptions (of 56 fields we could reconstruct the approximate location of 35 fields). 1) Ramat Hanadiv, 2) Mt. Gilboa, 3) Nahal Amud, 4) Rosh Pina, 5) Gamla, 6) Karei Deshe, 7) Kedoshim Forest, 8) Lehavim.



Fig. 2 Examples of the surveyed wild cereal habitats. **a)** A mixed stand of wild emmer and barley at Nahal Amud (AMU-01) associated with a rich herbaceous flora; **b)** a dense stand dominated by wild emmer at Mt. Gilboa (GIL-02); **c)** *Aegilops geniculata* dominating large parts of the herbaceous layer at Rosh Pina (ROS-01); **d)** the cleared cypress grove re-colonised by local grassland at Ramat Hanadiv (KEB-01) and dominated by *Avena sterilis*. Photos: A. Weide 2019.

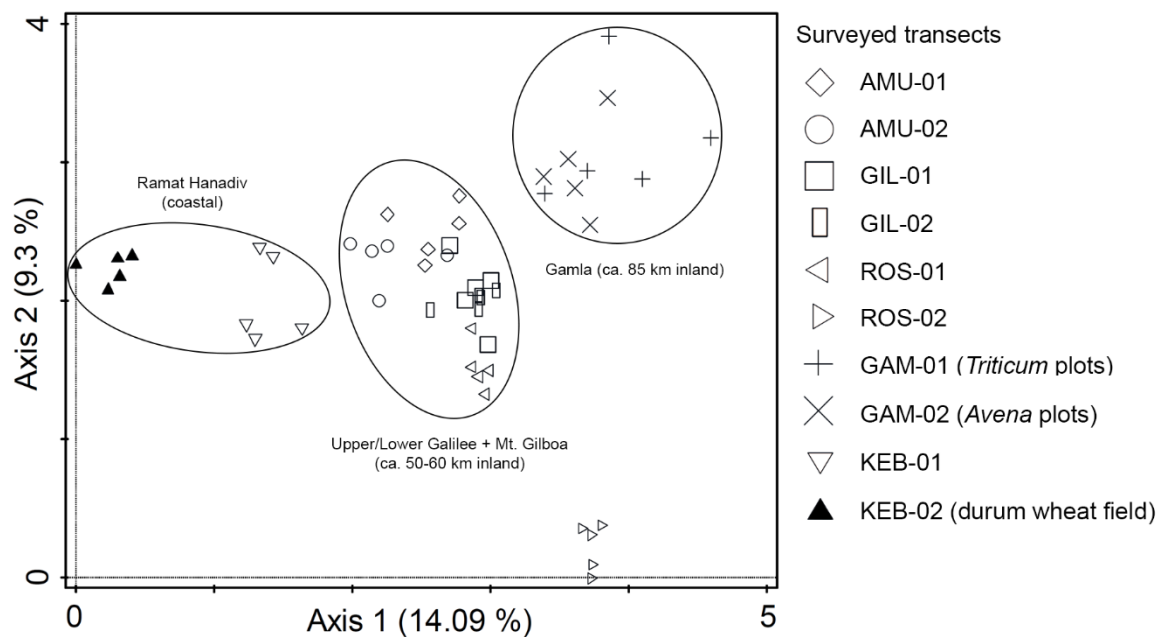


Fig. 3 Ordination diagram of a DCA based on 50 quadrats surveyed along ten transects in 2019 and 75 species. Percentages give the explained variation of the first two axes.

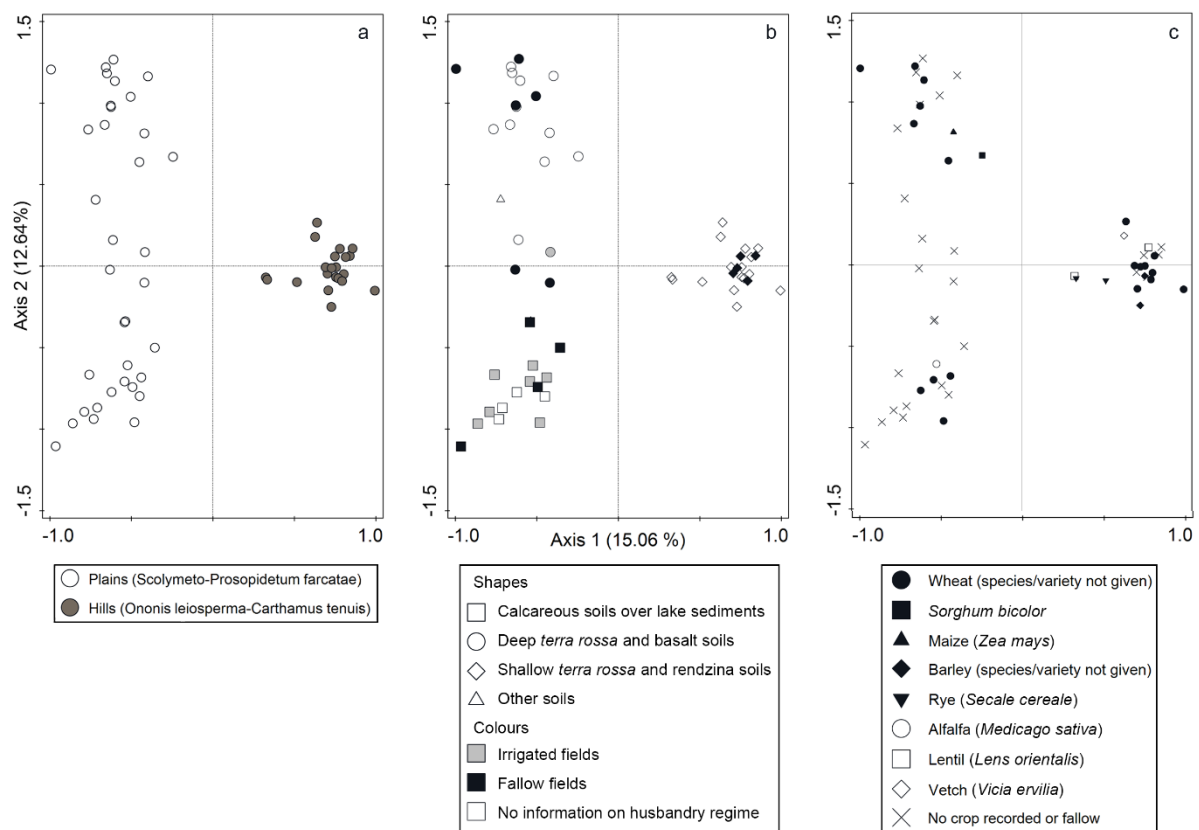


Fig. 4 Ordination diagram of a CA based on 56 fields and 80 species surveyed by Zohary (1950). **a)** phytosociological coding; **b)** coding after recorded soils and aspects of the husbandry regimes; **c)** coding after recorded crop species.

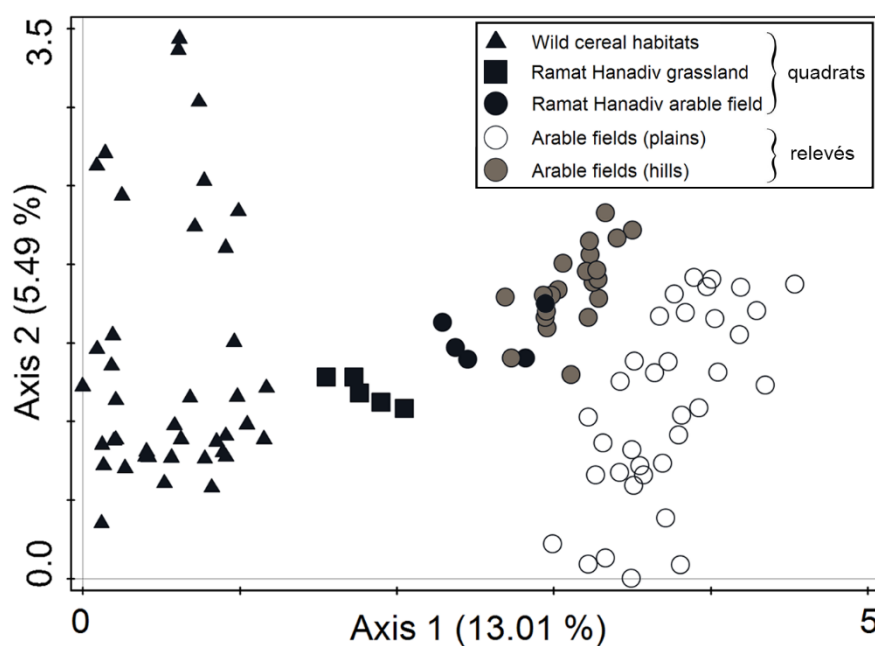


Fig. 5 Ordination diagram of a DCA based on 106 samples (quadrats/relevés) and 114 species comparing arable fields to wild cereal stands.

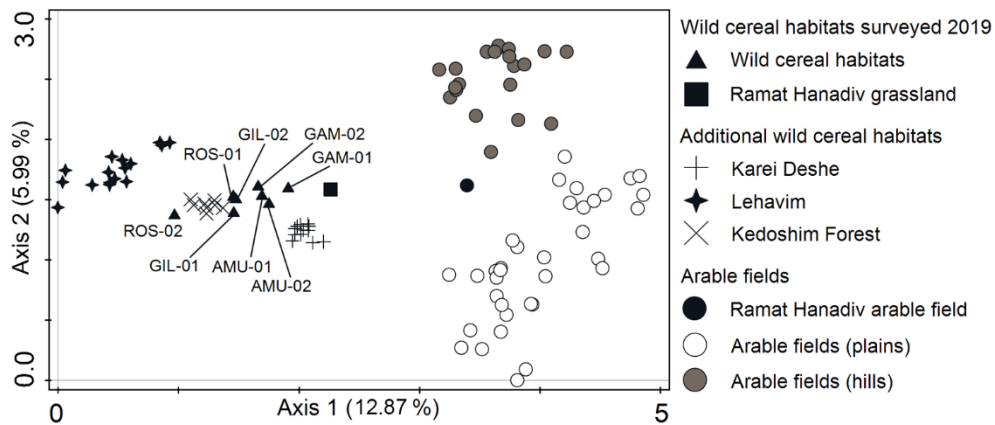


Fig. 6 Ordination diagram of a DCA based on 102 samples and 154 species including the three additional datasets for wild cereal habitats.

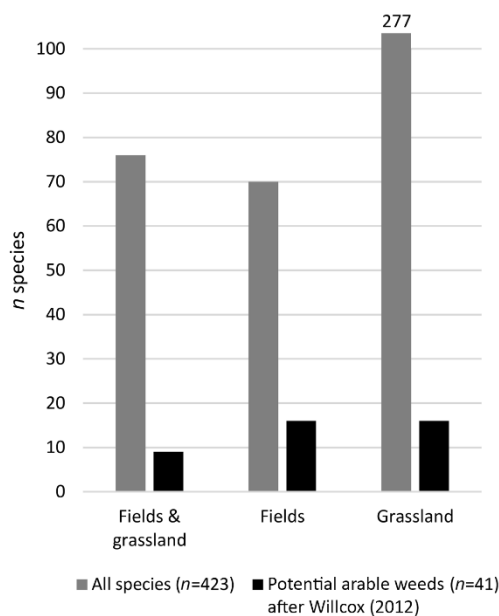


Fig. 7 The number of species that were only recorded in fields, grasslands or in both habitats. Quantification is based on all species or only those that belong to one of the potential arable weed taxa.

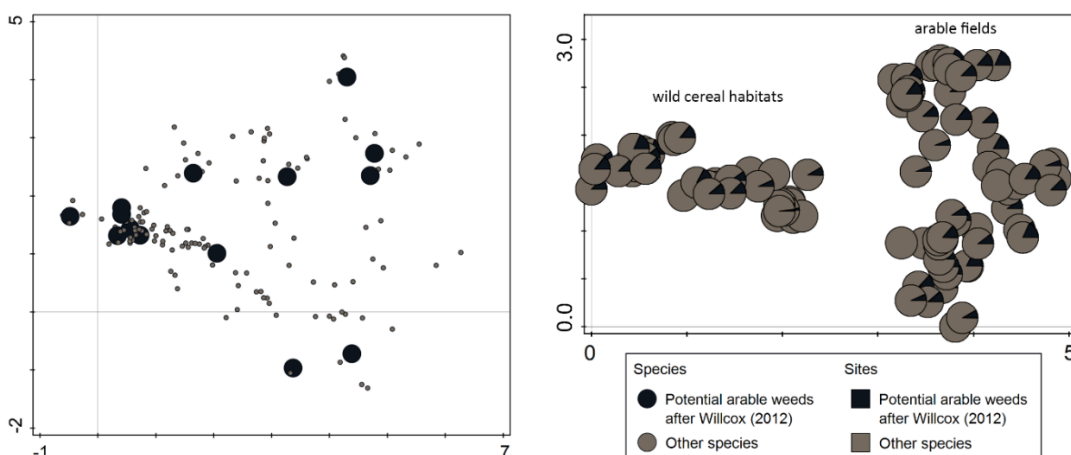


Fig. 8 Coding of variables and samples of the DCA shown in Fig. 6 after species that belong to the potential arable weed taxa ($n=14$). Pie charts give the proportion of potential arable weed species per site.

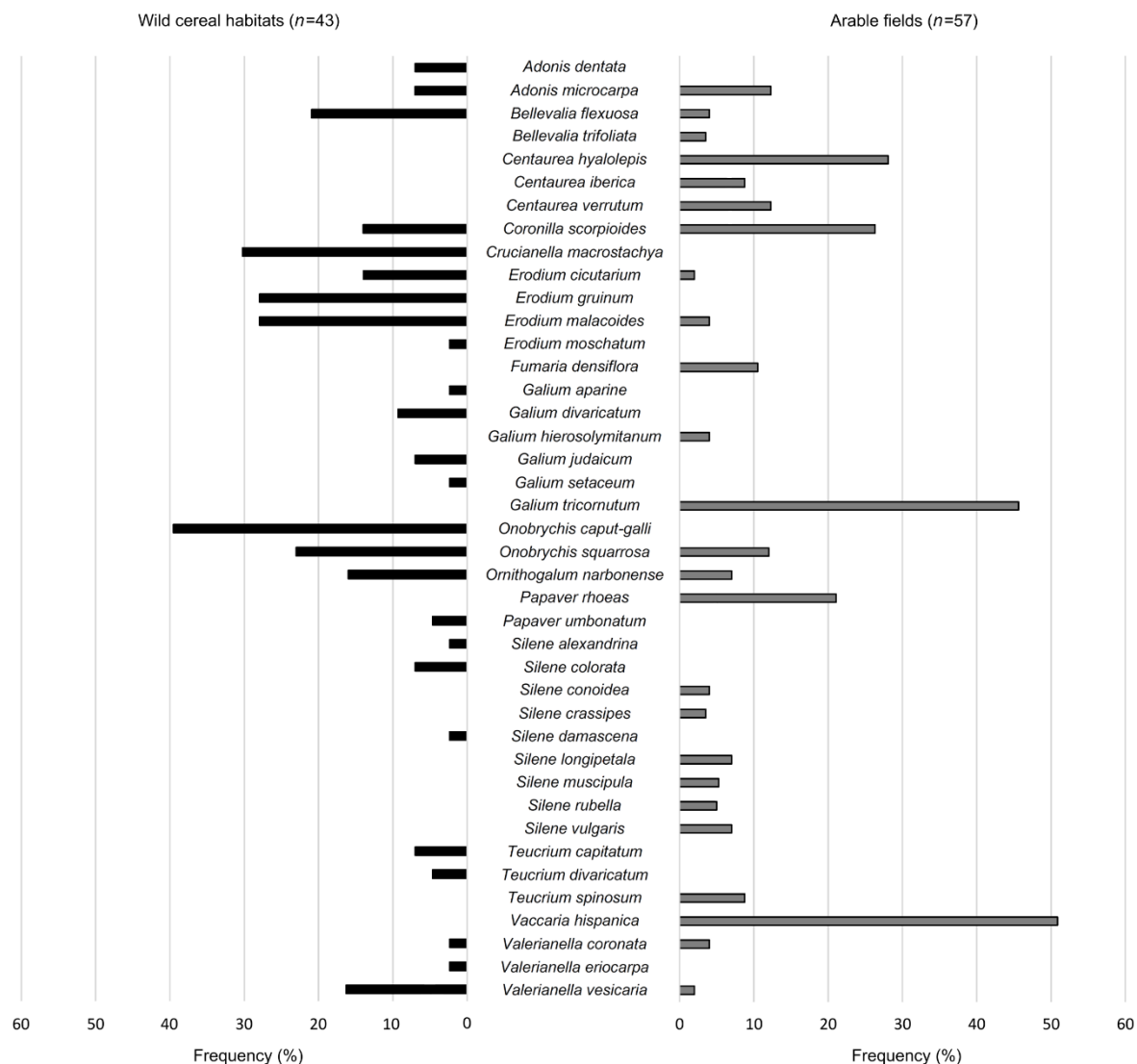


Fig. 9 Frequency of all recorded species belonging to the potential arable weed taxa ($n=41$) among wild cereal habitats and arable fields of the study region.

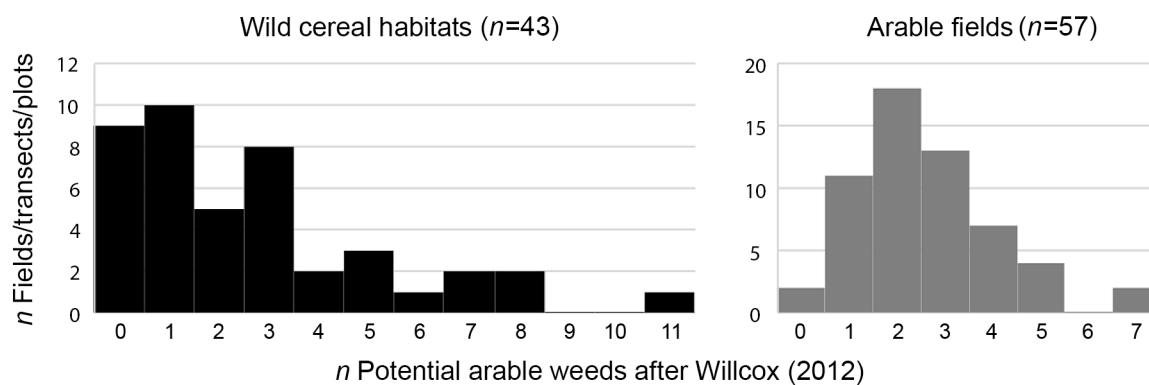


Fig. 10 Frequency distribution of the recorded species belonging to the potential arable weed taxa in wild cereal habitats and arable fields of the study region, each with a 5 % frequency cut-off.

Table 1 Survey sites and target species. Note that KEB-02 represents an arable field; the surveyed quadrats at Gamla are not placed along a transect but covering dense stands of *Triticum dicoccoides* (GAM-01) or *Avena sterilis* (GAM-02) in a plot covering ca. 0.23 ha.

Site	Rainfall ^a (mm)	Potential vegetation ^c	Transect codes	Elevation (m a.s.l.)	Transect length (m)	Target species				
						<i>A. sterilis</i>	<i>Ae. geniculata</i>	<i>H. v. spontaneum</i>	<i>T. t. dicoccoides</i>	<i>T. durum</i>
Nahal Amud (north of Kahal)	671	Savannoid grassland	AMU-01	134	33	X	X	X	X	
			AMU-02	140	37	X	X	X	X	
Mt. Gilboa	398	Park forest	GIL-01	426	65	X	X	X	X	
			GIL-02	415	70	X	X	X	X	
Rosh Pina	632 ^b	Park forest	ROS-01	482	20	X	X	X		
			ROS-02	490	25	X		X		
Gamla Nature Reserve	568	Park forest	GAM-01	420	Plot of	X			X	
			GAM-02	420	0.23 ha	X				
Ramat Hanadiv (above Kebara)	585	Park forest	KEB-01	112	60	X	X			
			KEB-02 (field)	120	126					X

^a long-term annual rainfall (1990-2019) of the nearest station, kindly provided by the Israel Meteorological Service; ^b 2005-2019; ^c after Danin (1988)

Table 2 Composition of life-forms and number of recorded species among the transects surveyed in 2019. Perennials exclude large shrubs or trees.

Transects	Annuals (%)	Perennials (%)	Species (n)
AMU-01	91.2	8.8	57
AMU-02	93	7	57
GIL-01	92.1	7.9	76
GIL-02	84.9	15.1	73
ROS-01	90.4	9.6	73
ROS-02	94.7	5.3	38
GAM-01	82	18	50
GAM-02	83.1	16.9	59
KEB-01	91.8	8.2	49
KEB-02 (field)	87.5	12.5	24

Table 3 All species recorded in wild cereal stands or arable fields that belong to the potential arable weed taxa.

Potential weed taxa after Willcox (2012)	Species recorded in wild cereal stands (n=25)	Species recorded in arable fields (n=25)
<i>Adonis</i>	<i>A. dentata</i> , <i>A. microcarpa</i> ^{a,b}	<i>A. microcarpa</i> ^{a,b}
<i>Bellevalia</i>	<i>B. flexuosa</i>	<i>B. flexuosa</i> , <i>B. trifoliata</i>
<i>Centaurea</i>	-	<i>C. hyalolepis</i> , <i>C. iberica</i> , <i>C. verrutum</i> ^a
<i>Coronilla</i>	<i>C. scorpioides</i>	<i>C. scorpioides</i>
<i>Crucianella</i>	<i>C. macrostachya</i>	-
<i>Erodium</i>	<i>E. cicutarium</i> , <i>E. gruinum</i> , <i>E. malacoides</i> , <i>E. moschatum</i>	<i>E. cicutarium</i> , <i>E. malacoides</i>
<i>Fumaria</i>	-	<i>F. densiflora</i>
<i>Galium</i>	<i>G. aparine</i> , <i>G. divaricatum</i> , <i>G. judaicum</i> , <i>G. setaceum</i>	<i>G. hierosolymitanum</i> , <i>G. tricornutum</i> ^a
<i>Glaucium</i>	-	-
<i>Gypsophila</i>	-	-
<i>Heliotropium</i>	-	-
<i>Onobrychis</i>	<i>O. caput-galli</i> , <i>O. squarrosa</i>	<i>O. squarrosa</i>
<i>Ornithogalum</i>	<i>O. narbonense</i> ^{a,b}	<i>O. narbonense</i> ^{a,b}
<i>Papaver</i>	<i>P. umbonatum</i>	<i>P. rhoeas</i> ^a
<i>Silene</i>	<i>S. alexandrina</i> , <i>S. colorata</i> , <i>S. damascena</i> ^{a,b}	<i>S. conoidea</i> , <i>S. crassipes</i> , <i>S. longipetala</i> , <i>S. muscipula</i> ^{a,b} , <i>S. rubella</i> , <i>S. vulgaris</i>
<i>Teucrium</i>	<i>T. capitatum</i> , <i>T. divaricatum</i>	<i>T. spinosum</i> ^a
<i>Thymelaea</i>	-	-
<i>Trigonella astroites</i>	-	-
<i>Vaccaria</i>	-	<i>V. hispanica</i> ^{a,b}
<i>Valerianella</i>	<i>V. coronata</i> ^{a,b} , <i>V. eriocarpa</i> , <i>V. vesicaria</i> ^{a,b}	<i>V. coronata</i> ^{a,b} , <i>V. vesicaria</i> ^{a,b}

^a listed as an obligatory weed by Willcox (2012) based on Zohary (1950); ^b occurs outside of arable fields based on records given in Danin and Orshan (1999)

Supplementary materials

Supplementary Table 1 Criteria used for proposing pre-domestication cultivation at Epipalaeolithic or Pre-Pottery Neolithic (PPN) sites in the Levant where cereal chaff is absent or consists of wild type rachises (smooth abscission scars indicative of brittle rachises).

Site (region) ^a	Dating (cal. BP) ^b	Proposed cultivars	Criteria used to propose pre-domestication cultivation				References
			Storage structures	Amount of grains ^c	Large 'cultivated sized' cereal grains	Potential arable weed flora	
Ohalo II (Upper Jordan Valley, Israel)	23,000	Wild barley, wild emmer				yes	Snir et al. (2015)
Jericho (Lower Jordan Valley, Palestine)	13,200-9,500	Wild barley, wild emmer	small bins		yes, but few grains		Hopf (1983)
'Iraq ed Dubb (Lower Jordan Valley, Jordan)	12,800-11,300	Wild einkorn				yes	Colledge (2001)
Mureybet (Upper Euphrates, Syria)	12,200-10,000	Wild einkorn (2-grained), wild barley				yes	Colledge (1998)
Dhra' (Lower Jordan Valley, Jordan)	11,700-11,200	Wild barley	granary and bins		yes	yes	Kuijt and Finlayson (2009), Colledge and Conolly (2018)
Gilgal (Lower Jordan Valley, Palestine)	11,500-11,100	Wild barley, wild oat	probably granary	yes			Weiss et al. (2006), Kuijt and Finlayson (2009), Kislev et al. (2010)
Jerf el Ahmar (Upper Euphrates, Syria)	11,400-10,600	Wild barley, wild einkorn (2-grained) or rye, wild lentil	cells in communal building containing cereal remains	yes (lentil)	yes	yes	Willcox et al. (2008), Willcox and Stordeur (2012)
Tell 'Abr (Upper Euphrates, Syria)	11,300-10,900	Wild einkorn (2-grained) or rye, wild lentil		yes (lentil)		yes	Willcox et al. (2008)
Netiv Hagdud (Lower Jordan Valley, Palestine)	11,300-10,800	Wild barley, wild lentil, <i>Vicia peregrina</i>	small bins and probably granary	yes		Yes (by Willcox 2012)	Bar-Yosef et al. (1991), Kislev (1997), Weiss et al. (2006), Melamed et al. (2008), Willcox (2012)

Supplementary Table 1 continued.

El-Hemmeh (Wadi el-Hasa, Jordan)	11,200-10,600	Wild barley		yes	yes	White and Makarewicz (2012)
Dja'de (Upper Euphrates, Syria)	11,100-10,300	Wild barley, wild einkorn (2-grained)/rye, wild lentil	yes (lentil)	yes	yes	Willcox et al. (2008)
Zahrat adh-Dhra' 2 (Lower Jordan Valley, Jordan)	11,100-10,400	Wild barley, wild pulses (lentil, various vetches)	yes (several pulse species)	yes		Edwards et al. (2004), Meadows (2004)

^a Note that we excluded several sites from this table. The evidence for cereal cultivation from late Epipalaeolithic Abu Hureyra presented by Hillman et al. (2001) was widely rejected (Nesbitt 2002; Colledge and Conolly 2010). Willcox (2012) compiled potential weed taxa for Dederiyeh Cave, Hallan Çemi and Tell Qaramel, but evidence for cultivation at both sites is limited to these potential weeds and was not supported in other publications (Savard et al. 2006; Willcox and Herveux 2012; Tanno et al. 2013).

^b Dates for the entire Epipalaeolithic/PPN occupation, not only for the period with proposed pre-domestication cultivation. Dates based on individual site reports and ex oriente: *PPND - The Platform for Neolithic Radiocarbon Dates*, 2020. Available from: http://www.exoriente.org/associated_projects/ppnd.php

^c The amount of recovered grains as an argument for pre-domestication cultivation is often connected to the (presumed) absence of suitable Late Pleistocene/Early Holocene wild cereal habitats or large legume populations in the vicinity of the respective sites (e.g. in Edwards et al. 2004; Weiss et al. 2006; Willcox et al. 2008). A consistent approach to use grain abundance – absolute numbers or relative amounts – as evidence for pre-domestication cultivation does not exist, which makes this criterion highly problematic due to its speculative nature.

Supplementary Table 2 Frequency of species that occur together in arable fields and wild cereal stands (blank rows) or only in arable fields (grey rows). Crops/wild cereals and large woody perennials were excluded.

Species	Frequency among all transects/relevés/plots (%)	
	Arable fields (n=76)	Wild cereal habitats (n=43)
<i>Adonis microcarpa</i>	12	7
<i>Ammi majus</i>	11	19
<i>Ammi visnaga</i>	12	5
<i>Anagallis arvensis</i>	37	60
<i>Anthemis pseudocotula</i>	35	2
<i>Beta vulgaris maritima</i>	12	30
<i>Brassica nigra</i>	2	23
<i>Bromus alopecuroides</i>	9	60
<i>Bupleurum subovatum</i>	68	2
<i>Carthamus glaucus</i>	12	35
<i>Carthamus tenuis</i>	40	23
<i>Cephalaria joppensis</i>	5	2
<i>Cichorium pumilum</i>	37	16
<i>Convolvulus arvensis</i>	51	2
<i>Convolvulus betonicifolius</i>	53	2
<i>Convolvulus pentapetaloides</i>	7	44
<i>Coronilla scorpioides</i>	26	14
<i>Cota palaestina</i>	18	19
<i>Crepis aspera</i>	14	21
<i>Cynodon dactylon</i>	39	28
<i>Daucus aureus</i>	21	5
<i>Eryngium creticum</i>	19	23
<i>Euphorbia arguta</i>	23	5
<i>Euphorbia falcata</i>	23	5
<i>Euphorbia helioscopia</i>	7	7
<i>Euphorbia peplus</i>	9	12
<i>Filago pyramidata</i>	5	16
<i>Geropogon hybridus</i>	30	51
<i>Gladiolus italicus</i>	9	5
<i>Glebionis coronaria</i>	19	2
<i>Gundelia tournefortii</i>	18	30
<i>Hedypnois rhagadioloides</i>	5	40
<i>Hymenocarpus circinnatus</i>	21	70
<i>Lolium rigidum</i>	18	63
<i>Lomelosia prolifera</i>	18	35
<i>Lotus palaestinus</i>	26	12
<i>Malcolmia crenulata</i>	19	2
<i>Malva multiflora</i>	2	14
<i>Medicago orbicularis</i>	11	5
<i>Medicago polymorpha</i>	14	21
<i>Medicago rotata</i>	9	19
<i>Medicago scutellata</i>	2	5
<i>Medicago turbinata</i>	18	2
<i>Misopates orontium</i>	7	5
<i>Notobasis syriaca</i>	11	44
<i>Onobrychis squarrosa</i>	9	23

Supplementary Table 2 continued.

<i>Ononis spinosa</i> subsp. <i>leiosperma</i>	35	5
<i>Ornithogalum narbonense</i>	7	16
<i>Orobanche crenata</i>	2	2
<i>Phalaris aquatica</i>	28	19
<i>Phalaris brachystachys</i>	33	7
<i>Phalaris paradoxa</i>	25	33
<i>Pimpinella cretica</i>	5	19
<i>Plantago afra</i>	16	19
<i>Prosopis farcta</i>	54	9
<i>Pterocephalus brevis</i>	7	12
<i>Rapistrum rugosum</i>	44	40
<i>Reseda alba</i>	5	2
<i>Rhagadiolus stellatus</i>	30	21
<i>Rostraria cristata</i>	12	19
<i>Scolymus maculatus</i>	51	33
<i>Scorpiurus muricatus</i>	32	23
<i>Senecio leucanthemifolius</i> subsp. <i>vernalis</i>	33	19
<i>Sinapis alba</i>	9	9
<i>Sinapis arvensis</i>	46	2
<i>Sonchus oleraceus</i>	5	16
<i>Trifolium campestre</i>	18	42
<i>Trifolium dasyurum</i>	9	9
<i>Trifolium purpureum</i>	9	30
<i>Trifolium resupinatum</i>	14	12
<i>Trifolium tomentosum</i>	5	16
<i>Trifolium vavilovii</i>	2	9
<i>Verbascum sinuatum</i>	12	2
<i>Vicia narbonensis</i>	25	5
<i>Vicia sativa</i>	11	5
<i>Ziziphora capitata</i>	7	5
<i>Alhagi graecorum</i>	12	0
<i>Alkanna galilaea</i>	9	0
<i>Allium schubertii</i>	14	0
<i>Anchusa azurea</i>	23	0
<i>Anchusa strigosa</i>	14	0
<i>Aristolochia maurorum</i>	11	0
<i>Asperula arvensis</i>	11	0
<i>Astomaea seselifolia</i>	18	0
<i>Bellevallia trifoliata</i>	4	0
<i>Bongardia chrysogonum</i>	18	0
<i>Bupleurum nodiflorum</i>	23	0
<i>Bupleurum odontites</i>	7	0
<i>Calepina irregularis</i>	5	0
<i>Campanula strigosa</i>	19	0
<i>Centaurea hyalolepis</i>	28	0
<i>Centaurea iberica</i>	9	0
<i>Centaurea verrutum</i>	12	0
<i>Cephalaria syriaca</i>	37	0
<i>Cerastium dichotomum</i>	11	0

Supplementary Table 2 continued.

<i>Chrozophora tinctoria</i>	21	0
<i>Cynara syriaca</i>	26	0
<i>Eminium spicatum</i>	7	0
<i>Eruca vesicaria</i>	12	0
<i>Erucaria hispanica</i>	16	0
<i>Euphorbia aleppica</i>	5	0
<i>Euphorbia valerianifolia</i>	7	0
<i>Exoacantha heterophylla</i>	5	0
<i>Fumaria densiflora</i>	11	0
<i>Galium tricornutum</i>	46	0
<i>Gladiolus atrovioleaceus</i>	9	0
<i>Haplophyllum buxbaumii</i>	7	0
<i>Hypericum triquetrifolium</i>	33	0
<i>Kickxia elatine</i>	7	0
<i>Kruberia peregrina</i>	2	0
<i>Lathyrus gloeospermus</i>	2	0
<i>Lathyrus ochrus</i>	5	0
<i>Legousia pentagonia</i>	9	0
<i>Leontice leontopetalum</i>	9	0
<i>Linaria halepensis</i>	7	0
<i>Linum mucronatum</i>	5	0
<i>Lolium temulentum</i>	33	0
<i>Lotus conjugatus</i> subsp. <i>requienii</i>	2	0
<i>Malva trimestris</i>	21	0
<i>Malvella sherardiana</i>	7	0
<i>Medicago blanchiana</i>	9	0
<i>Melilotus indicus</i>	18	0
<i>Moluccella laevis</i>	7	0
<i>Ononis hirta</i>	11	0
<i>Ononis pubescens</i>	7	0
<i>Onosma gigantea</i>	2	0
<i>Papaver rhoeas</i>	21	0
<i>Phlomis herba-venti</i> subsp. <i>pungens</i>	16	0
<i>Polygonum bellardii</i>	5	0
<i>Prangos ferulacea</i>	9	0
<i>Ranunculus arvensis</i>	25	0
<i>Ranunculus marginatus</i>	7	0
<i>Ridolfia segetum</i>	28	0
<i>Salvia dominica</i>	9	0
<i>Scandix palaestina</i>	2	0
<i>Scolymus hispanicus</i>	7	0
<i>Silene crassipes</i>	4	0
<i>Silene longipetala</i>	7	0
<i>Silene muscipula</i>	5	0
<i>Silene vulgaris</i>	7	0
<i>Stachys zohariana</i>	2	0
<i>Teucrium spinosum</i>	9	0
<i>Tordylium aegyptiacum</i>	9	0
<i>Vaccaria hispanica</i>	51	0

Supplementary Table 2 continued.

<i>Vicia villosa</i>	2	0
<i>Warburgina faktorovskyi</i>	5	0

Supplementary text 1: the increase in potential weeds in archaeobotanical assemblages from the late Younger Dryas and the Early Holocene

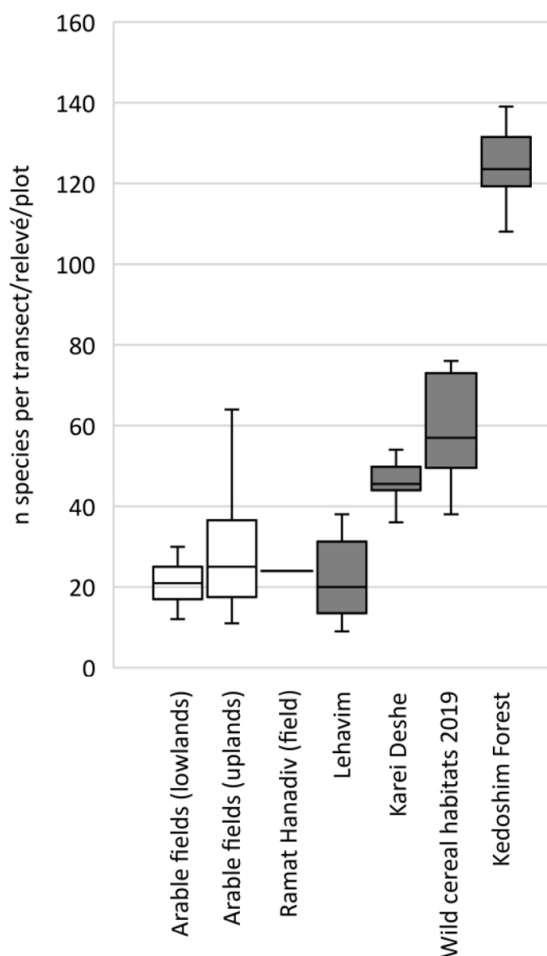
Willcox (2012) argued that sites dating to the Younger Dryas and the Early Holocene contain more potential arable weed taxa than earlier sites, which he took as evidence for the beginnings of cultivation (see figure 1 in Willcox 2012). There are several problems with this assumption. First, Epipalaeolithic sites from which abundant macrobotanical remains were recovered are very rare. An increased incorporation of potential weed seeds into Younger Dryas and Early Holocene plant assemblages – as opposed to earlier sites – is an unverified hypothesis and only based on comparisons to a few Epipalaeolithic datasets. The proposed increase of weeds is based on two to three sites including the early Epipalaeolithic camp site of Ohalo II and the late Epipalaeolithic cave occupation at Dederiyeh Cave. Both sites provided low numbers of potential weed taxa (2 and 6, resp., according to Willcox 2012) but also represent very different contexts compared to the large-scale tell excavations from where the increased abundance of weeds (between 10 to 20) on later sites was inferred. Whether the higher diversity in some Younger Dryas and Early Holocene archaeobotanical assemblages reflects larger excavation areas and more permanent occupations is unclear. Secondly, the increased occurrence of potential weeds at sites dating to the Younger Dryas and Early Holocene may also be due to changing subsistence practices and more intensive grassland exploitation strategies other than cultivation. All sites in question provide abundant evidence for the regular exploitation of cereals but distinguishing cereal gathering from cultivation based on a taxonomic assessment would require a comparison between clearly gathered assemblages and clearly cultivated assemblages. However, this is not possible to date because of the lack of macrobotanical remains from most Epipalaeolithic sites. The assumption that *genera*, which represent weeds on Bronze Age agricultural sites, should also represent weeds at Late Natufian and PPNA sites is further flawed by the fact that these genera include many non-arable species. It must be emphasised that until now almost every Epipalaeolithic site with abundant cereal remains was proposed as a candidate for pre-domestication cultivation based on – among other features – an associated *potential* weed flora (e.g. Abu Hureyra 1, Dederiyeh, Ohalo II) (Hillman et al. 2001; Willcox 2012; Snir et al. 2015). This can also be taken as a sign that *potential* weed floras occur at every site where wild cereal communities have been exploited, because many facultative weeds originate from grasslands and were – deliberately or accidentally – transported to settlements with the cereal harvests.

Supplementary text 2: data preparation for multivariate analysis

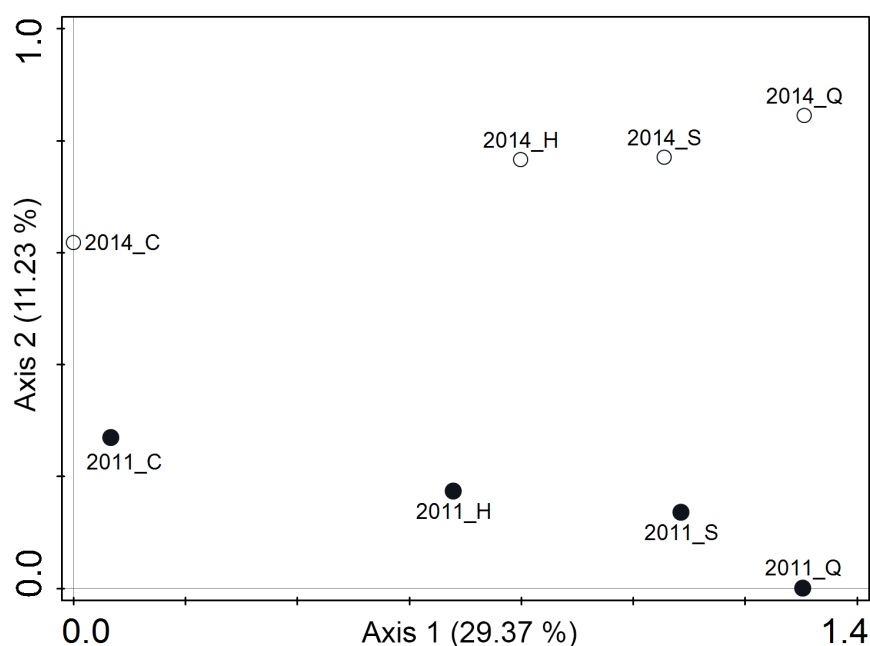
Rare species were excluded because multivariate analyses are sensitive to rare observations that can affect general trends in the produced ordination diagrams (Jones 1991; Smith 2014). However, the exclusion of too many species can also change relationships between samples. In order to mediate between these two effects, cut-offs to exclude rare species were determined for each analysis using the following procedure: several ordination diagrams showing the first two axes were created with increasing species frequency cut-offs between 5 and 10 %. For each analysis we chose the threshold that allowed for the exclusion of as many rare species as possible before relationships between – and variability within – groups changed significantly.

Supplementary text 3: floristic composition of the wild cereal communities from Karei Deshe, Kedoshim Forest and Lehavim

Species richness of the three additional wild cereal communities varied considerably with Lehavim having the smallest number of species comparable to arable fields while Kedoshim Forest harboured the richest communities (Supplementary Figure 1). Among all selected plots and years, the community at Lehavim contained 97.5 % annuals, Kedoshim Forest 73.7 % annuals and Karei Deshe 70.5 % annuals. Prior to the integration into our dataset, we used correspondence analysis to explore intra-site variation between plots/transects and years. A clear pattern of floristic change was only evident at Kedoshim Forest, where plots surveyed two and five years after tree removal, respectively, were separated along axis 2, while axis 1 separated the four sampled plots (Supplementary Figure 2). This intra-site variation did not affect the relation of Kedoshim Forest to the other wild cereal habitats or arable fields, as the Kedoshim plots consistently cluster in Fig. 6 (see main text). Moreover, the samples from Karei Deshe and Lehavim did not cluster according to plots or years (diagrams not shown). This indicates that rainfall variation has a minor impact on species composition, at least within the sampling periods of four to six years, as the last sampling year at Karei Deshe (2019) received twice as much rainfall than the previous years (822 mm vs. 329-475 mm) and the last sampling year at Lehavim experienced a harsh drought (40 mm vs. long-term average of 295 mm).



Supplementary Figure 1 Species richness of the surveyed arable fields (white) and wild cereal habitats (grey).



Supplementary Figure 2 Ordination diagram of a DCA based on 8 plots and 194 species (25 % cut-off) from Kedoshim Forest.

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