



**HAL**  
open science

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

Alexander Weide, Laura Green, John Hodgson, Carlyne Douché, Margareta Tengberg, Jade Whitlam, Guy Dovrat, Yagil Osem, Amy Bogaard

► **To cite this version:**

Alexander Weide, Laura Green, John Hodgson, Carlyne 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-03941959v1>**

Submitted on 7 Feb 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

2 **Asia**

3

4 Alexander Weide<sup>a\*</sup>, Laura Green<sup>a</sup>, John G. Hodgson<sup>a,b</sup>, Carolyne Douché<sup>c</sup>, Margareta Tengberg<sup>c</sup>, Jade  
5 Whitley<sup>a</sup>, Guy Dovrat<sup>d</sup>, Yagil Osem<sup>e</sup>, Amy Bogaard<sup>a</sup>

6

7 <sup>a</sup> School of Archaeology, University of Oxford, Oxford, UK

8 <sup>b</sup> Department of Archaeology, University of Sheffield, Sheffield, UK

9 <sup>c</sup> Muséum National d'Histoire Naturelle, CNRS, Paris, France

10 <sup>d</sup> Department of Natural Resources, Newe-Ya'ar Research Center, Agricultural Research Organiza-  
11 tion, Ramat Yishay, Israel

12 <sup>e</sup> Department of Natural Resources, Agricultural Research Organization, Volcani Center, Bet-Dagan,  
13 Israel

14

15 \* corresponding author; ORCID: <https://orcid.org/0000-0002-0358-9995>

16

17

18

19

20

21

22

23

24

25

26

## 27 **Abstract**

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

40

## 41 **1. Introduction**

42 The protracted domestication model for the origins of plant cultivation and domestication in south-  
43 west Asia posits that wild cereals and pulses were cultivated for at least 1000-2000 years prior to the  
44 appearance of morphologically differentiated domesticated crops in the archaeological record<sup>1-3</sup>.  
45 Snir *et al.*<sup>4</sup> even suggested wild cereal cultivation around the Last Glacial Maximum, 23,000 years  
46 ago, at Ohalo II on the Sea of Galilee. This prolonged phase of wild plant cultivation is termed ‘pre-  
47 domestication cultivation’ (PDC) and inferred through different lines of evidence, including large  
48 quantities of cereal or pulse grains<sup>1,5</sup>, increased grain sizes<sup>6-8</sup>, the presence of substantial storage  
49 facilities<sup>9,10</sup>, and the occurrence of crop progenitors outside of their natural distribution range<sup>1</sup>. The  
50 most direct evidence to suggest wild plant cultivation is, however, based on genera that include ara-  
51 ble weed species<sup>1,4,7,8,11-13</sup>. Associations of seeds and fruits from these potential arable weed genera  
52 with large amounts of wild cereal and pulse remains at archaeological sites are commonly interpret-

53 ed as indicative of increased levels of disturbance due to vegetation clearance and soil tillage<sup>11-13</sup>,  
54 which generally feature as the defining aspects of cultivation as a subsistence practice<sup>14</sup>. This high-  
55 lights that the formation of early arable weed floras is thought to reflect agricultural disturbances, as  
56 opposed to other common disturbance factors in Mediterranean grasslands like summer-droughts,  
57 grazing, and wildfires<sup>15</sup>. The increased sizes of wild cereal grains at some sites are also conventionally  
58 attributed to soil disturbance, due to the expectation that larger grains and their large seedlings  
59 have competitive advantages in open environments and when buried deeper<sup>16,17</sup>. Although cereal  
60 grain size increases were possibly related to other factors as well, such as variable water availability  
61 when sown on different soils or fluctuating levels of atmospheric CO<sub>2</sub> during the Early Holocene<sup>1,18</sup>,  
62 most authors attributed the combination of potential arable weeds and increasing grain sizes to cul-  
63 tivation in disturbed arable habitats. PDC is therefore understood, often explicitly, as entailing rela-  
64 tively labour-intensive practices comparable to developed agricultural systems, including vegetation  
65 clearance and annual cycles of soil tillage, sowing, probably weeding, and harvesting<sup>5,10-12,17</sup>. This cur-  
66 rent understanding of PDC diverges from other models for emerging plant management practices  
67 around the world, which emphasise the viability of low-input strategies for facilitating the abun-  
68 dance of exploitable resources that do not rely on increased levels of disturbance<sup>19-21</sup>. Importantly ,  
69 associating labour-intensive agricultural practices with PDC has profound socio-economic implica-  
70 tions because tillage demands increased inputs of labour and energy into units of land from which  
71 food is obtained. Increasing social complexity and labour inputs into arable land therefore feature as  
72 fundamental socio-economic developments entangled with the emergence of domesticated  
73 crops<sup>17,19,22</sup>.

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

79 mous cultivation experiments by G.C. Hillman and M.S. Davies<sup>23</sup>, who showed that annual cereal cul-  
80 tivation that employs harvesting techniques like uprooting or sickle reaping would automatically se-  
81 lect for non-shattering ears and could theoretically lead to a non-shattering population in decades or  
82 a few centuries. The millennia-long PDC phase contradicts this hypothesis, also as the use of sickles  
83 as harvesting tools is well attested archaeologically during the Late Pleistocene and Early Holocene<sup>3</sup>.  
84 To resolve this discrepancy between archaeological observations and theoretical expectations, re-  
85 searchers have proposed various scenarios to explain why the proportions of non-shattering spike-  
86 lets never exceeded that of modern wild populations despite millennia of PDC. These include har-  
87 vesting semi-ripe ears to prevent grain loss through shattering, ground collection of shed spikelets to  
88 maximize yields, the continuous cultivation of wild cereals in the same fields, where the shattered  
89 spikelets contribute significantly to the population in the following year, and collecting grains from  
90 unmanaged populations for replenishing seed stocks after failed harvests<sup>1,17,23,24</sup>. All these strategies  
91 would maintain high proportions of shattering spikelets in the managed populations, suppressing  
92 selection for non-shattering phenotypes. Alternatively, Asouti<sup>18</sup> suggested that plant cultivation  
93 would not have been a resilient strategy during the climatically unstable Early Holocene, prompting  
94 human communities to frequently focus on alternative resources which would have interrupted and  
95 possibly reversed selection for domestication traits. However, except for harvesting semi-ripe ears<sup>3</sup>,  
96 all these explanations are speculative and not based on direct archaeological evidence. As a result,  
97 specific practices associated with PDC, and their socio-economic significance, remain unknown, as  
98 do the factors that inhibited selection for domestication traits during millennia of PDC.

99 Weide et al.<sup>25</sup> provided empirical evidence which suggests that the conventional taxonomic ap-  
100 proach to identifying early arable weed floras, and with this the emergence of cultivation systems  
101 that involve regular soil disturbance, is fundamentally flawed. Many arable species originated in non-  
102 arable southwest Asian grasslands that are dominated by cereal crop progenitors<sup>26</sup>. Consequently,  
103 the seeds and fruits of potential weed genera at key PDC sites could likewise derive from non-arable  
104 species or facultative weeds harvested with wild cereals in local non-arable grasslands<sup>25,27,28</sup>. If the

105 associated exploitation practices did not include annual cycles of tillage and sowing but rather fo-  
106 cused on strategies that maintained low levels of disturbance and relied on self-sowing of the tar-  
107 geted species, the absence of selection for domestication traits would be expected rather than being  
108 anomalous<sup>23</sup>. To test whether the proposed weed floras from Late Pleistocene and Early Holocene  
109 PDC sites reflect such non-arable grassland communities, we need to reconstruct disturbance levels  
110 much more precisely than is possible with the taxonomic approach currently used. Analysing the  
111 composition of plant functional traits related to agroecological variables such as mechanical soil dis-  
112 turbance offers a promising solution to these problems and has proven useful in reconstructing  
113 management regimes and associated practices in the past<sup>29,30</sup>.

114

#### 115 **Distinguishing arable from non-arable habitats using functional ecology**

116 Plant functional traits occur in limited sets of combinations globally<sup>31</sup> and can be used to assess, for  
117 example, how ecological parameters affect species distribution and determine community  
118 assembly<sup>32</sup>. In applying functional ecology to arable weed floras, certain sets of functional traits suc-  
119 cessfully distinguished between relatively high- and low-intensity cultivation regimes in temperate  
120 and Mediterranean Europe, northern Africa, and in archaeological contexts<sup>30,33-36</sup>. Moreover, our  
121 functional ecological approach is suited to overcoming shortcomings of the conventional taxonomic  
122 approach to the identification of early cultivation and associated practices. First, functional analyses  
123 of archaeobotanical assemblages are based on species from individual samples or contexts rather  
124 than an arbitrary selection from all identified *potential* weed taxa of a site<sup>33,37</sup>. This has the ad-  
125 vantage of selecting weed species based on their co-occurrence with crops or target species that  
126 dominate individual samples, which does not *a priori* exclude edible weed species and results in a  
127 more accurate identification of ancient weed floras. Second, in building a functional model based on  
128 modern survey data, we can differentiate ecological conditions along a continuous spectrum and  
129 locate archaeobotanical samples along this ecological continuum. As opposed to the conventional  
130 taxonomic approach, this goes beyond the dichotomous distinction between gathered and cultivat-

131 ed archaeobotanical assemblages. Third, these sample-by-sample functional analyses provide a reli-  
132 able estimate of the variability of practices within a prehistoric human community and the oppor-  
133 tunity to analyse this variability in its specific socio-economic context and over time<sup>36</sup>.

134 The modern arable weed floras analysed in this study (Fig. 1) developed under 'traditional' husband-  
135 ry regimes in Palestine during the first half of the twentieth century as part of the *musha'a* land ten-  
136 ure system (Zohary 1950). The *musha'a* was characterised by two-field rotation with a winter cereal  
137 or legume on one field and a summer crop of sesame or durrah (*Sorghum bicolor*) on a second field  
138 that remained fallow during the rainy period<sup>26,38</sup>. Irrigation and manuring played limited roles, but  
139 fallow fields were tilled up to three times during the fallow period using animal-drawn ards (or  
140 'scratch-plows')<sup>39</sup>. The sampled non-arable habitats (Fig. 1; Table 1) are all dominated by southwest  
141 Asian cereal crop progenitors (*Hordeum vulgare* subsp. *spontaneum*, *Triticum turgidum* subsp. *dicoc-*  
142 *coides*) and related, large-seeded grasses (*Aegilops geniculata*, *Ae. peregrina*, *Avena sterilis*, *Horde-*  
143 *um bulbosum*). None of the sampled wild cereal habitats were cultivated during the last ca. 50 years;  
144 nor were they exposed to regular grazing, which reduces the density of wild cereal stands and se-  
145 lects for shorter small-seeded species<sup>40,41</sup>. The only exceptions are Karei Deshe, with a medium  
146 stocking rate of 0.55 cows per hectare, and Lehavim, where a flock of ca. 600 sheep continuously  
147 grazed plots during winter/spring, resulting in a reduction of large-seeded grasses (see Methods sec-  
148 tion).

149 Here we use flowering duration and the ability of perennials to readily regenerate from root and rhi-  
150 zome fragments, traits that are positively related to high levels of mechanical soil disturbance<sup>29,30</sup>, to  
151 build a functional ecological model that differentiates between disturbance regimes of the surveyed  
152 arable and non-arable habitats (Supplementary Table 1). Annual and perennial species that flower  
153 rapidly and over an extended period have a higher probability of regenerating from seeds in regimes  
154 of high disturbance<sup>15</sup>. Similarly, perennials that rapidly regenerate from root and rhizome fragments  
155 perform well under conditions of high mechanical disturbance, which even facilitates their growth<sup>42</sup>.

156 These traits were related to conditions of high mechanical disturbance in different climatic and eco-

157 logical settings, including England<sup>35</sup>, Greece<sup>30</sup>, Spain<sup>43</sup>, and Morocco<sup>34</sup>, demonstrating that they func-  
158 tion independently from local environmental conditions and are applicable to archaeological con-  
159 texts<sup>33-35</sup>.

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

179

## 180 **2. Results**

### 181 *Distinguishing modern wild cereal habitats from arable fields*



182 Modern arable weed floras and wild cereal communities in the Mediterranean and Irano-Turanian  
183 phytogeographical regions of the southern Levant were clearly separated based on species composi-  
184 tion (Fig. 2a). A detrended correspondence analysis (DCA) using semi-quantitative data (species  
185 presence/absence), based on 156 samples (transects and plots) from arable fields ( $n=61$ ) and non-  
186 arable wild cereal habitats ( $n=97$ ) with 150 species, separated both groups along axis 1. Weide et  
187 al.<sup>25</sup> showed that this clear separation is based on the ecological conditions in the arable and non-  
188 arable habitats, related to local land-use practices, and is not induced by different survey periods or  
189 methods. The floristic variation within both groups reflects a combination of factors related to topo-  
190 graphic and edaphic conditions and differences in the local vegetation<sup>25,26</sup>. Coding species according  
191 to the duration of their flowering period shows that long-flowering species (>5 months) occur in  
192 higher proportions in the arable fields compared to the non-arable grassland communities, which  
193 support more short-flowering species (<3 months) (Fig. 2b). Figure 2c shows that perennials which  
194 readily regenerate from root and rhizome fragments also reach higher proportions in the arable  
195 fields, confirming that readily regenerating and long flowering species are suited to indicate differ-  
196 ences in disturbance conditions between arable and non-arable habitats (see Supplementary Figure  
197 7 for species plots of the DCA coded according to the two functional traits).

198 We used discriminant analysis (DA) to distinguish between the modern arable and non-arable com-  
199 munities based on semi-quantitative data (presence/absence). In a first DA we used flowering dura-  
200 tion and vegetative regeneration as the discriminating variables (DA1; Supplementary Table 4). Sup-  
201 plementary Fig. 8a shows the discriminant function extracted from DA1 that correctly reclassified  
202 90.2% of all modern samples. The two traits discriminate between arable and non-arable communi-  
203 ties as predicted, with arable weed floras characterised by species that regenerate from vegetative  
204 organs fragmented by tillage (roots, rhizomes) and/or seeds produced before a mechanical disturb-  
205 ance event such as tillage or weeding disrupted their life cycle (flowering duration) (Supplementary  
206 Fig. 8b). A small number of samples was incorrectly reclassified as deriving from either a non-arable  
207 grassland community ( $n=6$  or 9.8% of arable fields) or an arable field ( $n=7$  or 9.9% of non-arable

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

215 One disadvantage with using this combination of traits is that samples without perennials are omit-  
216 ted from the analysis as they did not receive an attribute score for vegetative regeneration. This ex-  
217 cluded 26 samples from non-arable habitats, including 63% of the samples from Lehavim. We there-  
218 fore repeated the DA with flowering duration as the only discriminating variable (DA2). The discrimi-  
219 nant function extracted from DA2 correctly reclassified 86.7% of all samples and maintained the  
220 general trends of all sample groups (Fig. 3a; Supplementary Table 4). The number of samples incor-  
221 rectly reclassified increased among the arable fields ( $n=9$  or 14.8%) and grasslands ( $n=12$  or 12.4%)  
222 (Table 2). Moderately to heavily grazed plots were again correctly reclassified as non-arable, con-  
223 firming that both functions discriminate between communities in tilled and non-tilled habitats inde-  
224 pendently from local grazing regimes.

225

### 226 ***Disturbance regimes associated with pre-domestication cultivation***

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

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

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

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

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

269 Samples from Jerf el Ahmar show no increase in discriminant scores throughout the three occupa-  
270 tion phases, with the only positive outlier dating to the earliest occupation phase (Fig. 3e). The doc-  
271 umented size increase in barley and einkorn grains throughout the occupation of the site<sup>6</sup> therefore  
272 seems to be related to factors other than deeper burial conditions in tilled soils, supporting recent  
273 studies that raised doubts over a general relationship between soil disturbance and selection for  
274 larger seeds<sup>49</sup>. Large-seeded phenotypes have strong competitive advantages under conditions of  
275 high interspecific competition due to their higher germination success and larger plant size<sup>50</sup>. Under  
276 conditions of relatively low soil disturbance, selection for larger seeds could in part be linked to the-  
277 se competitive advantages gained through seed size enlargement, resulting in larger seedlings that  
278 can more optimally exploit the increasingly productive conditions during the Early Holocene and sur-  
279 rounding human habitations<sup>50</sup>.

280

### 281 **3. Discussion**

#### 282 ***The ecology of pre-domestication cultivation***

283 In ecological terms, vegetation clearance and soil tillage have the primary goals of establishing an  
284 arable field that gives the sown grains a competitive advantage and release resources for growth<sup>14,51</sup>.

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

286 harvested wild cereals indicates that their exploitation strategies did not require frequent mechani-  
287 cal disturbance of the soil and the complete removal of competing vegetation to favour wild cereals.  
288 We suggest that this is due to their adaptive syndrome, summarised recently by Wood and Lenné<sup>28</sup>  
289 as consisting of large seeds in awned spikelets that facilitate quick burial in the soil and contribute to  
290 the ability of the wild cereals to form dense stands and dominate annual grasslands. A key trait of  
291 this adaptive syndrome is the comparatively large size of the grains of cereal crop progenitors, which  
292 produce large seedlings that are very competitive and provide a high fitness in annual plant commu-  
293 nities<sup>47,50</sup>. The key to understand the low disturbance levels in the exploited wild cereal habitats  
294 therefore is that regular soil tillage and the clearance of vegetation would not be necessary for giving  
295 wild cereals an advantage over other species. These patterns suggest that human communities at  
296 sites such as Jerf el Ahmar, Dja'de, Netiv Hagdud, or Gilgal I based their strategies of maintaining rich  
297 and exploitable wild cereal populations on the ecological strategies and the high competitiveness of  
298 the cereals themselves. This may have included the active re-sowing of stands and their protection  
299 from large grazers, practices that are widely documented ethnographically<sup>20</sup>. In addition, our find-  
300 ings illustrate that the potential weed floras that accompany wild cereals in archaeological contexts  
301 do not represent arable communities but rather the floristic composition of untilled grasslands, har-  
302 vested together with the cereals<sup>25</sup>.

303 Low levels of mechanical disturbance associated with 'pre-domestication cultivation' do not auto-  
304 matically explain the absence of selection for domestication traits, because annual cycles of sowing  
305 and harvesting could impose selection pressures even in the absence of frequent soil tillage<sup>23</sup>. How-  
306 ever, annual sowing is a mere expectation of the PDC model and not evidenced by independent da-  
307 ta. On the contrary, P. Anderson argued that annual sowing is by no means necessary to maintain  
308 rich wild cereal stands<sup>52</sup>. This is based on field observations, including harvesting of wild cereal  
309 stands in Syria and the establishment of an experimental wild cereal population in France. In both  
310 contexts, self-sowing of shattering phenotypes was sufficient for producing a rich stand in the year  
311 after the population was harvested. Combined with the low disturbance levels associated with PDC

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

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

322 These findings urge us to reconsider the concept of 'pre-domestication *cultivation*' in southwest Asia  
323 as the beginnings of arable farming. Instead, it is plausible to assume that the associated 'low-  
324 disturbance' or 'no tillage' management practices were oriented to the ecology of existing cereal  
325 populations and aimed at creating and maintaining dense populations. Comparable ecological mod-  
326 els exist for the development of close human-plant relationships all around the world<sup>53-55</sup>, highlight-  
327 ing that emerging domestication processes are generally grounded in ecological collaborations be-  
328 tween humans and other organisms<sup>21,56</sup>.

329

### 330 ***Disturbance as a function of socio-economic change***

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

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

340 At Jerf el Ahmar, several subterranean circular structures indicate the construction of communal  
341 buildings where food resources were stored in clay storage bins (Fig. 3e)<sup>10</sup>. The last communal build-  
342 ing constructed at Jerf el Ahmar did not contain storage bins anymore and the mode of food storage  
343 during the final occupation phase is generally unclear, echoing the situation at Dja'de (Fig. 3d)<sup>57,58</sup>.  
344 The 'kitchens' at Jerf el Ahmar, rooms with accumulations of food processing and preparation im-  
345 plements that are only found in some buildings, further indicate that food storage, processing, and  
346 consumption retained a strong communal element<sup>10</sup>. All these patterns reflect a strong focus on  
347 communal social and economic activities on the Middle Euphrates.

348 Excavations at Gilgal I and Netiv Hagdud revealed structures that imply a comparable focus on com-  
349 munal socio-economic strategies in the Jordan valley. These include structure 11 at Gilgal I, a non-  
350 residential building that contained the large hoard of stored barley and oat grains included in our  
351 functional analyses (Fig. 3f)<sup>5,59</sup>, and possible clay storage silos with diameters between 1–3m at Netiv  
352 Hagdud (Fig. 3g)<sup>60</sup>. That the structures from Netiv Hagdud represent extramural storage silos is sup-  
353 ported by the discovery of comparable silos with suspended floors at Dhra' and Wadi Faynan 16 on  
354 the eastern side of the Jordan valley, indicating a regional pattern where extramural silos were used  
355 as communal granaries<sup>8,9</sup>. These silos, together with the location of food processing and preparation  
356 facilities inside and outside of residential structures<sup>61</sup>, likewise suggest a communal organisation of  
357 cereal exploitation, storage, processing, and consumption activities at key PDC sites in the southern  
358 Levant<sup>9</sup>. The general absence of grave goods and a lack of indicators for the individual accumulation  
359 of material wealth during much of the Levantine PPN situate this communal organisation of cereal  
360 exploitation in a pan-regional socio-economic system that strongly emphasised group cohesion and  
361 identity at the expense of individuality<sup>62</sup>. In this light, the absence of systematic tillage in communal-  
362 ly organised cereal exploitation systems also reflects a lack of social and economic incentives to in-

363 vest higher amounts of labour into subsistence practices, as individual persons or families would not  
364 have benefitted from increased labour investments<sup>63</sup>.  
365 This changed with the gradual emergence of household-centred farming communities from the early  
366 and middle PPNB, between ca. 10,700–9,500 cal. BP, which developed increasingly ‘private’ systems  
367 of food storage, processing, and consumption<sup>46,61,64</sup>. The increased levels of soil disturbance at  
368 Çatalhöyük reflect a developed phase of this intensification of crop cultivation, where individual  
369 households stored their own harvests and directly benefitted from their investments into agricultural  
370 labour (Fig. 3b)<sup>36,46</sup>. Increasing labour investments and the associated acceleration of soil disturb-  
371 ance conditions can therefore be seen as a function of limited sharing networks and emerging ‘pri-  
372 vate’ ownership over cultivated foods in early farming societies.

373

#### 374 **4. Methods**

##### 375 ***Study sites and survey methods***

376 We analysed floristic and functional trait data from non-arable wild cereal habitats and arable fields  
377 in the Mediterranean and Irano-Turanian phytogeographical regions<sup>65</sup> of northern and central Israel.  
378 The eight wild cereal habitats have a Mediterranean climate but differed in their long-term mean  
379 annual precipitation, elevation, and the dominant grass species (Tab. 1). They were selected based  
380 on several criteria: the presence and dominance of at least one large-seeded grass species, the ab-  
381 sence of cultivation during the last ca. 50 years and regular grazing. The only exceptions to this were  
382 Karei Deshe near the Sea of Galilee and Lehavim in the northern Negev (see below).

383 Survey methods and periods differed between the wild cereal habitats (see also Weide *et al.*<sup>25</sup>). At  
384 Nahal Amud, Rosh Pina, Mt. Gilboa, Gamla, and Ramat Hanadiv (Fig. 1b), we surveyed the vegetation  
385 in plots following the method described by Jones *et al.*<sup>66</sup> and adjusted by Bogaard *et al.*<sup>34</sup>. In each  
386 plot we recorded all species in five 1m<sup>2</sup> quadrats along a linear transect. In contrast to arable fields,  
387 the extent of the surveyed plots is defined by the local topography (roads, rock outcrops) and  
388 changes in the vegetation (forest margins). Oriented on these natural boundaries, we placed the 20-



389 70m long transects along the longitudinal axis of the studied plots and away from roads and forest  
390 margins to avoid edge effects. The surveyed area at Gamla represents the only exception to this lay-  
391 out, where we surveyed one 0.23 ha large plot and placed five quadrats each in isolated patches of  
392 dense *Triticum turgidum* subsp. *dicoccoides* (GAM-01) or *Avena sterilis* (GAM-02) stands.

393 From the surveys conducted at Karei Deshe Experimental Farm, located north of the Sea of Galilee  
394 near Chorazim (Fig. 1b), we selected survey data from two plots of 31.1 and 28.2 ha. These plots  
395 were sampled each year between 2014-2019 and had a continuous moderate stocking rate (0.55  
396 cows ha<sup>-1</sup> year<sup>-1</sup>). The vegetation was sampled along four and five transects, respectively, using the  
397 step-point method<sup>67</sup>. It has been acknowledged that this method misses rare species and can under-  
398 estimate species richness<sup>68</sup>, however, as we describe below, for the statistical analyses we excluded  
399 rare species from all datasets.

400 The selected plots from the long-term ecological research (LTER) site of Kedoshim Forest in the Jeru-  
401 salem Mountains (Fig. 1b) represent cleared plots in a *Pinus halepensis* plantation<sup>69</sup>. The four 20\*20  
402 m plots we selected for this study were completely cleared from trees in 2009 and sampled in 2011  
403 and 2014. All species were recorded using a nested sampling strategy in each 10 m<sup>2</sup> corner of the  
404 four plots, with scales of 10\*10 cm, 30\*30 cm and 1\*1m.

405 The selected dataset from the LTER site of Lehavim in the Goral Hills, northern Negev (Fig. 1b), de-  
406 rives from eight 10\*10 m plots located on the wadi shoulders. Four plots were protected from graz-  
407 ing during the entire survey period between 1996-1999, whereas the other four plots were continu-  
408 ously grazed by a flock of ca. 600 Awassi sheep between January–May and August–December<sup>70</sup>. This  
409 heavy grazing pressure resulted in the reduction of large-seeded grasses, such as *A. sterilis*, *Hordeum*  
410 *vulgare* subsp. *spontaneum*, and *T. turgidum* subsp. *dicoccoides*. Every year, all species were record-  
411 ed in four to five 20\*20 cm quadrats per plot.

412 We used M. Zohary's arable weed surveys as a comparative dataset for local arable environments<sup>26</sup>  
413 (Fig. 1b). Zohary surveyed arable fields in Mandatory Palestine during the first half of the twentieth  
414 century, where he recorded relevés covering a total of 100m<sup>2</sup> per field. The fields were managed as

415 part of the *musha'a* land tenure system, which involved tilling of fields up to three times during the  
416 fallow periods<sup>38</sup>. These 'cultivated' or 'bare' fallows are thought to maintain productivity under semi-  
417 arid conditions by enhancing soil water retention, fertility, and controlling competition with  
418 weeds<sup>39,51</sup>. The most common tillage implements used in the region during the sampling period were  
419 animal-drawn ards, also called scratch ploughs, which were used to till fields in remote and hilly lo-  
420 cations, whereas tractor ploughing was restricted to lowland arable fields<sup>26,39</sup>. However, tractors  
421 were only introduced to Mandatory Palestine during the 1920s and did not play a large role in the  
422 local *musha'a* during the sampling period<sup>71</sup>, indicating that the sampled arable weed floras formed  
423 under non-mechanised tillage regimes. Zohary divided the recorded weed floras into associations  
424 characteristic for a particular environmental setting. We used his detailed survey data for two weed  
425 associations, both located in the Mediterranean and Irano-Turanian phytogeographical regions. The  
426 Scolymeto-Prosopidetum *faricatae* characterised fields in plains and intermountain valleys on deep  
427 *terra rossa*, basalt and calcareous soils (labelled "plains"). In contrast, the *Ononis leiosperma*-  
428 *Carthamus tenuis* grew in fields with much shallower *terra rossa* and rendzina soils that were locat-  
429 ed on terraces and small patches in mountainous settings (labelled "hills")<sup>72</sup>.  
430 We recorded the weed flora of one arable field at Ramat Hanadiv in 2019 (Fig. 1b), where durum  
431 wheat was cultivated without the aid of pesticides or fertilisers. The grains are sown in December  
432 and not harvested in the following spring but eaten by local wildlife (mainly gazelle and boar). The  
433 remaining stubble is ploughed under with a tractor around October, which represents the only major  
434 anthropogenic disturbance.

435

### 436 ***Plant functional traits***

437 To distinguish between arable and non-arable habitats we used the two functional traits flowering  
438 duration and vegetative regeneration. Both traits relate to the species' potential of rapid regenera-  
439 tion under conditions of high mechanical disturbance in arable environments<sup>29,30,35</sup>.

440 Flowering duration is positively associated with conditions of high and unpredictable disturbance  
441 such as soil tillage<sup>15</sup>. Annuals and perennial species without extensive rhizomes that flower over ex-  
442 tended periods begin to flower rapidly and simultaneously produce seeds, assuring reproduction in  
443 years when unpredictable disturbance events disrupt the life cycle early<sup>73</sup>. In addition, the ability to  
444 produce multiple generations during a vegetation period adds to the success of long-flowering spe-  
445 cies in environments that are subjected to unpredictable disturbances. Flowering duration, meas-  
446 ured as the maximum number of months a species flowers, therefore is a useful indicator for the  
447 conditions of mechanical disturbance in a given environment. However, as climatic factors influence  
448 flowering duration, this trait must be measured in the study area. As this is usually not possible in  
449 practice, we extracted flowering duration from the regional floras, *Flora Palaestina*<sup>74</sup> and *Flora of*  
450 *Turkey*<sup>75</sup>. When archaeological weed seeds were only identified to the genus level but all regional  
451 species in this genus have a comparable flowering period, we used the average flowering period of  
452 all species.

453 The capacity of perennials to regenerate rapidly after mechanical disturbance events is associated  
454 with the presence of extensive root, rhizome, or stolon systems, and their ability to form new vege-  
455 tative shoots from root or stem fragments<sup>42,76</sup>. However, not all perennial species with rhizomes or  
456 stolons can rapidly regenerate after mechanical disturbance events. For example, *Urtica dioica* or  
457 *Phragmites australis* develop extensive clonal patches but are not well adapted to conditions of high  
458 disturbance<sup>15</sup>. Large terminal tubers and vertical tap roots can be classified as stationary sensu  
459 Håkansson<sup>42</sup> and are equally sensitive to conditions of high disturbance. We classified species after  
460 their capacity to rapidly regenerate under conditions of high mechanical disturbance as  
461 *no/moderate capacity* (stationary perennials and perennials with extensive root or stem systems  
462 that are sensitive to disturbance) and *rapidly regenerating* (perennials that have extensive root or  
463 stem systems and rapidly regenerate from fragments). This classification is based on field observa-  
464 tions and local floras<sup>74,75</sup>.

465

466 ***Selection of archaeobotanical samples and weed taxa***

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

476 Green<sup>37</sup> conducted the taphonomic analyses and selection of weed taxa for the samples from  
477 Çatalhöyük, Dja'de, and Jerf el Ahmar. All samples from Çatalhöyük represent storage contexts<sup>36</sup>,  
478 whereas the samples from Dja'de and Jerf el Ahmar derive from primary contexts (hearths and floor  
479 layers) and secondary deposits (building collapse, midden deposits). The selected samples from  
480 Dja'de and Jerf el Ahmar were originally analysed by Willcox *et al.*<sup>1</sup> and Douché<sup>77</sup>. The status of non-  
481 crop taxa as weed contaminants was confirmed via a crop processing analysis detailed in<sup>37,78</sup>, indicat-  
482 ing that the analysed samples from these sites represent crop processing by-products. Weed assem-  
483 blages from processing by-products *can* be biased towards long-flowering species, while weeds in  
484 processing products may contain more short-flowering species<sup>79</sup>. However, as all analysed samples  
485 represent by-products, such a bias can be ruled out for comparing conditions of disturbance at  
486 Çatalhöyük, Dja'de, and Jerf el Ahmar. Based on the crop-processing analysis, combined with the  
487 frequency and ecology of wild species in the assemblages, taxa that were likely gathered or repre-  
488 sent ruderals were excluded for Çatalhöyük (*Descurainia sophia*, *Helianthemum sp.*, *Teucrium sp.*),  
489 Dja'de (*Alyssum/Lepidium*, *Atriplex sp.*, *Capparis sp.*, *Hyoscyamus sp.*, *Stipa sp.*), and Jerf el Ahmar  
490 (*Capparis sp.*) (for details see Green<sup>37</sup>). Dung-derived taxa identified through previous taphonomic  
491 analyses were excluded from the samples of Çatalhöyük<sup>80,81</sup>. Despite evidence for cattle manage-

492 ment and morphological changes at Dja'de<sup>82</sup>, dung burning as a significant factor in the formation of  
493 the earlier assemblages can be ruled out based on the rarity of small and hard-coated seeds that  
494 typically survive ruminant digestion<sup>37,83</sup>.

495 The analysed samples from Atlit-Yam derived from a submerged well and we defined each layer  
496 from this well as one sample. Two layers that did not contain enough weed seeds were combined to  
497 one sample (210–230 cm and 230–150 cm)<sup>44</sup>. No weed species were excluded from this dataset, as  
498 all remains were identified to the species level and represent obligatory or facultative arable weeds.  
499 For Netiv Hagdud, Kislev<sup>84</sup> summarised samples as per locus, which means that the samples we ana-  
500 lysed represent loci and not individual archaeobotanical samples. We excluded all potential weeds  
501 that were not identified to the species or genus level, all rare taxa (present in only 1 locus), and the  
502 potential cultivars/target species (*Avena* spp., *Hordeum vulgare* subsp. *spontaneum*, *Triticum tur-*  
503 *gidum* subsp. *dicoccoides*, *Lathyrus* spp., *Lens* sp., *Vicia ervilia*).

504 The assemblage from Gilgal I derives from a single storage context dominated by wild barley and oat  
505 grains<sup>85</sup>. The contaminants of the sample are most likely weeds harvested with the cereals, from  
506 which we excluded imprecise identifications (only Viciaeae), genus identifications where life history is  
507 unclear (*Alopecurus* sp.), and the potential cultivars/target species (*Avena sterilis*, *Hordeum vulgare*  
508 subsp. *spontaneum*, *Triticum turgidum* subsp. *dicoccoides*, *Lens* sp.).

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

517 (*Atriplex leucoclada*, *A. rosea*, *Puccinellia* cf. *convoluta*, *Suaeda palaestina/fructicosa*)<sup>48,86</sup>, and (2) the  
518 potential weed assemblage selected by Snir et al.<sup>4</sup>.

519

### 520 **Data analysis**

521 All analyses were performed using semi-quantitative datasets (presence/absence of species per  
522 sample), which has been shown to be as effective in distinguishing arable fields and different cultiva-  
523 tion regimes as fully quantitative data<sup>43,87</sup>. The floristic composition of individual sites and their rela-  
524 tionship to each other was explored via correspondence analysis (CA) using CANOCO 5<sup>88</sup>. Prepara-  
525 tion of floristic datasets for CA, including standardising the taxonomy and determining frequency  
526 cut-offs for excluding rare species (we used 7% in the CA shown in Fig. 2), is detailed in Weide et  
527 al.<sup>25</sup>. As sample distribution was potentially biased by the arch-effect, we detrended the ordination  
528 model by segments using a detrended correspondence analysis (DCA)<sup>88</sup>.

529 We used discriminant analysis to distinguish modern arable and non-arable habitats according to  
530 their disturbance conditions using IBM SPSS version 27. For this we determined an average score per  
531 functional trait for each sample (quadrat/relevé/plot) as follows:

532

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

533

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

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

546

547

#### 548 **Acknowledgements**

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

554

#### 555 **Author Contributions**

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

561

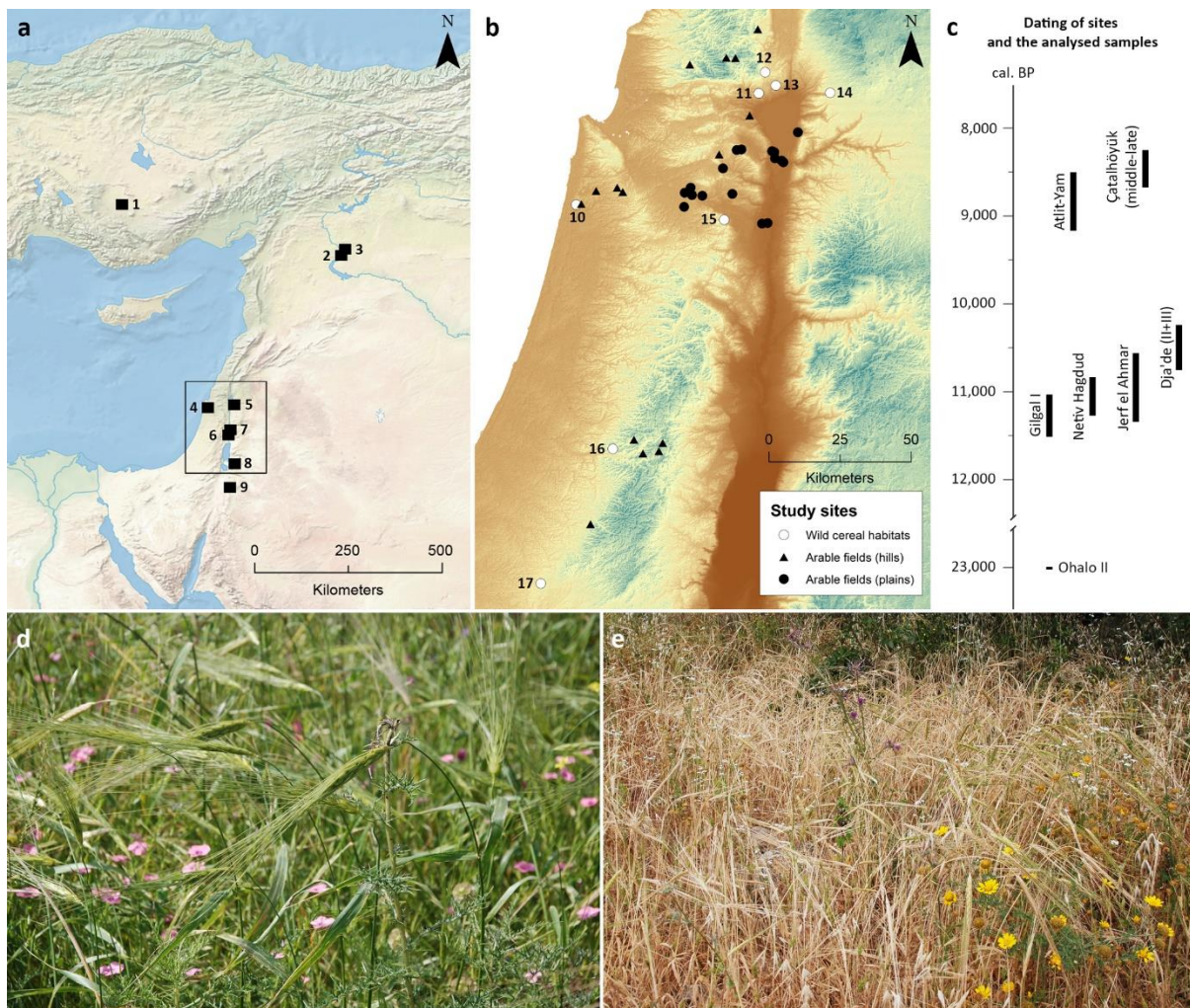
#### 562 **Competing Interests Statement**

563 We have no competing interests.

564

#### 565 **Data Availability Statement**

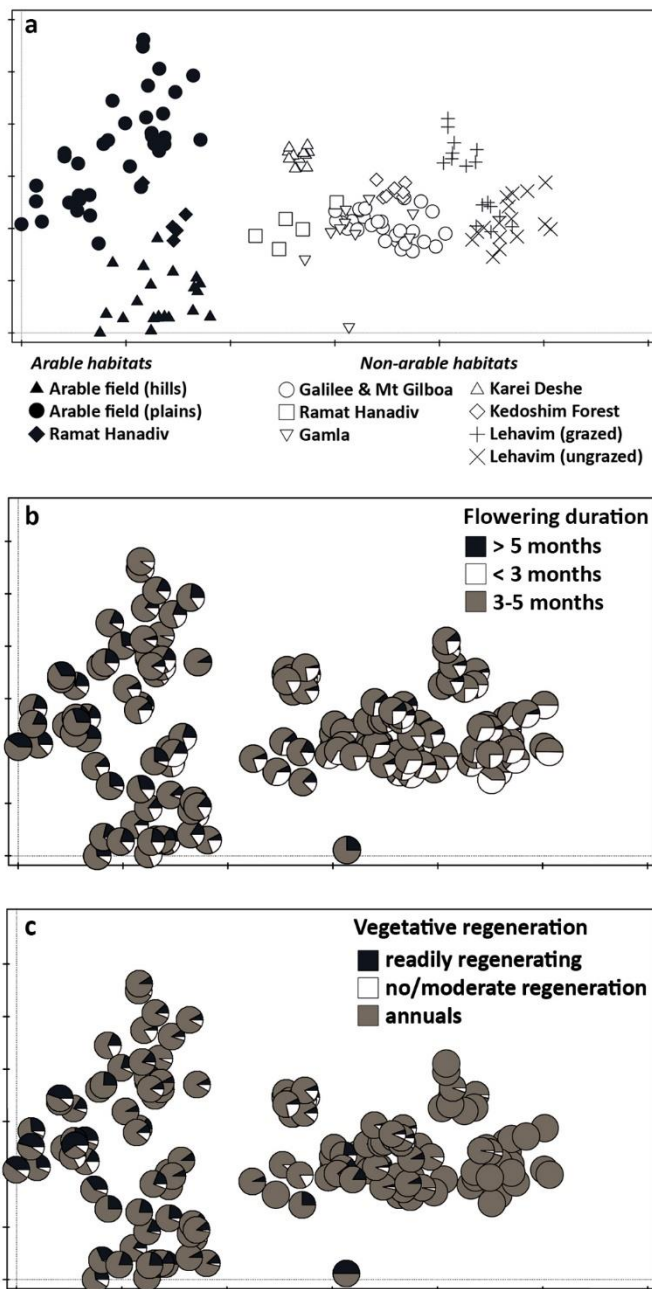
566 All data used to perform the discriminant analyses and their outputs are given in the supplementary  
 567 materials. The modern floristic datasets and the archaeobotanical data analysed during the current  
 568 study are not publicly available due to ongoing analyses of the samples and raw data. Upon comple-  
 569 tion of all analyses the raw datasets will be made publicly available. Parts of the modern floristic da-  
 570 taset are available from the corresponding author on reasonable request. The raw data on which  
 571 the analyses from Çatalhöyük are based are fully published and publicly accessible in Green (2017).  
 572



573  
 574 **Fig. 1** a) Location of archaeological sites mentioned in the text; b) Location of arable fields and non-  
 575 arable wild cereal habitats; c) Chronology of the archaeological sites and samples analysed in the  
 576 study; note that Dja'de and Çatalhöyük were occupied for longer but not all phases are represented  
 577 by the analysed samples; d) wild emmer wheat (*T. turgidum* subsp. *dicoccoides*) near the Sea of Gali-



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.  
 583



**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.

600

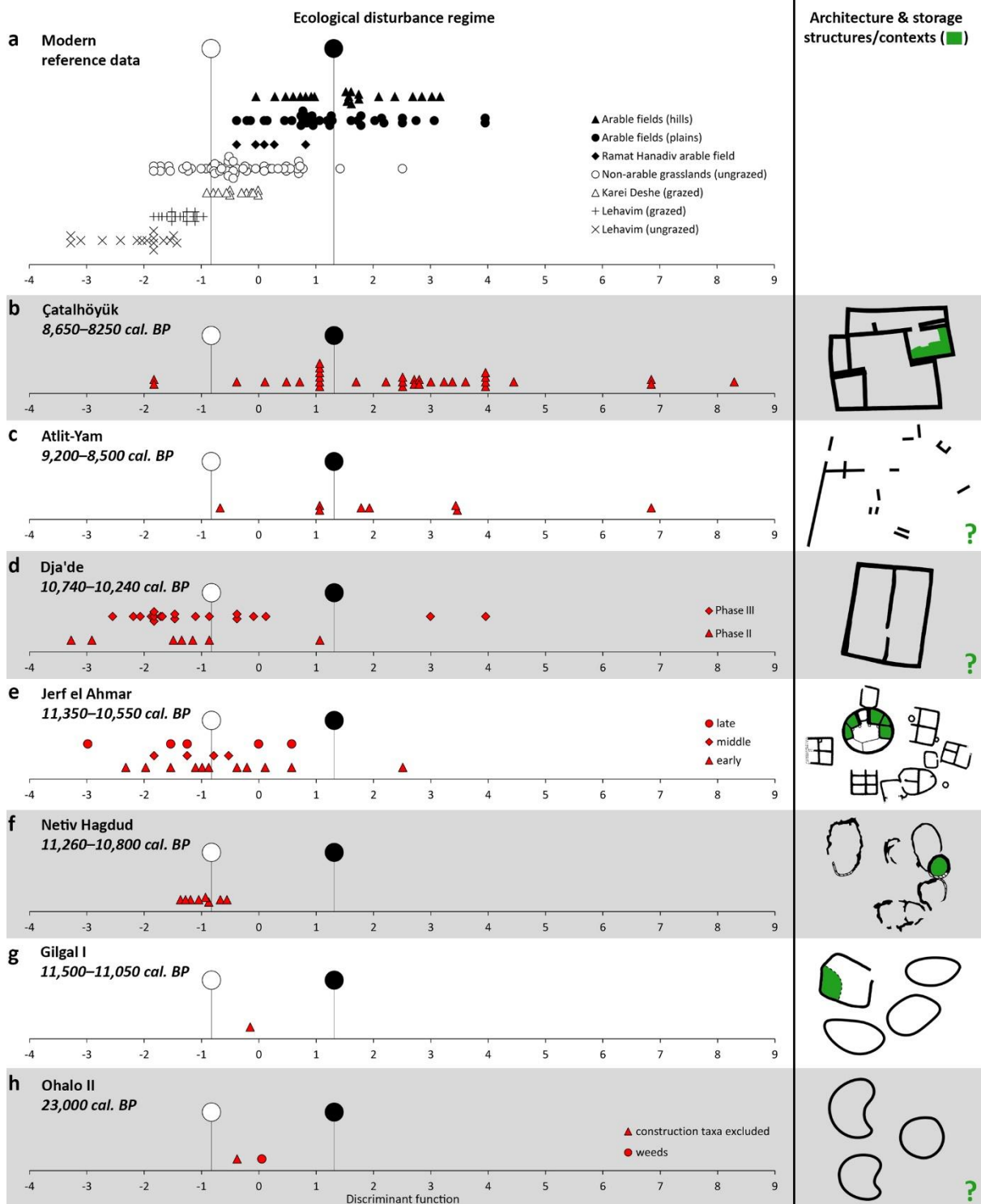
601

602

603

604

605



606

607 **Fig. 3** Discriminant function extracted from the discriminant analysis using only flowering duration as  
 608 a discriminating variable; the archaeobotanical samples (in red) are correlated with an example of  
 609 the typical residential architecture (not to scale) of the analysed settlement phases and storage facil-  
 610 ities (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.<sup>46</sup>; **c**) samples from Atlit-Yam and parts of the settle-  
614 ment plan (storage mode unclear), redrawn from Galili et al.<sup>89</sup>; **d**) samples from Dja'de with building  
615 EA6 (phase II, storage mode unclear), redrawn from Douché<sup>58</sup>; **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.<sup>90</sup>; **f**) samples from Netiv Hagdud and parts of the settlement plan with a  
618 potential free-standing storage silo, redrawn from Bar-Yosef and Gopher<sup>60</sup>; **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.<sup>91</sup>; **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.<sup>48</sup>.

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

Site	Elevation (m a.s.l.)	MAP <sup>a</sup> (mm)	Soil	Potential vegetation <sup>b</sup>	Survey method <sup>c</sup>	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 <sup>d</sup>	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 <sup>a</sup> long-term mean annual precipitation of the nearest station, kindly provided by the Israel Meteorological Service; <sup>b</sup> after Danin<sup>65</sup>; <sup>c</sup> see Methods for further details; <sup>d</sup>  
624 here *Aegilops peregrina*

625

626

627

628

629

630

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

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

648

649

650

651

652

653

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

654

655

656

657

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



662 **References**

- 663 1 Willcox, G., Fornite, S. & Herveux, L. Early Holocene cultivation before domestication in  
664 northern Syria. *Vegetation History and Archaeobotany* **17**, 313-325, doi:10.1007/s00334-  
665 007-0121-y (2008).
- 666 2 Fuller, D. Q., Willcox, G. & Allaby, R. G. Cultivation and domestication had multiple origins:  
667 arguments against the core area hypothesis for the origins of agriculture in the Near East.  
668 *World Archaeology* **43**, 628-652, doi:10.1080/00438243.2011.624747 (2011).
- 669 3 Ibáñez, J. J., Anderson, P. C., González-Urquijo, J. & Gibaja, J. Cereal cultivation and  
670 domestication as shown by microtexture analysis of sickle gloss through confocal  
671 microscopy. *Journal of Archaeological Science* **73**, 62-81,  
672 doi:<https://doi.org/10.1016/j.jas.2016.07.011> (2016).
- 673 4 Snir, A. *et al.* The Origin of Cultivation and Proto-Weeds, Long Before Neolithic Farming.  
674 *PLOS ONE* **10**, e0131422, doi:10.1371/journal.pone.0131422 (2015).
- 675 5 Weiss, E., Kislev, M. E. & Hartmann, A. Autonomous Cultivation Before Domestication.  
676 *Science* **312**, 1608-1610, doi:10.1126/science.1127235 (2006).
- 677 6 Willcox, G. Measuring grain size and identifying Near Eastern cereal domestication: evidence  
678 from the Euphrates valley. *Journal of Archaeological Science* **31**, 145-150,  
679 doi:<http://dx.doi.org/10.1016/j.jas.2003.07.003> (2004).
- 680 7 White, C. E. & Makarewicz, C. A. Harvesting practices and early Neolithic barley cultivation at  
681 el-Hemmeh, Jordan. *Vegetation History and Archaeobotany* **21**, 85-94, doi:10.1007/s00334-  
682 011-0309-z (2012).
- 683 8 Colledge, S., Conolly, J., Finlayson, B. & Kuijt, I. New insights on plant domestication,  
684 production intensification, and food storage: the archaeobotanical evidence from PPNA  
685 Dhra'. *Levant* **50**, 14-31, doi:10.1080/00758914.2018.1424746 (2018).
- 686 9 Kuijt, I. & Finlayson, B. Evidence for food storage and predomestication granaries 11,000  
687 years ago in the Jordan Valley. *Proceedings of the National Academy of Sciences* **106**, 10966-  
688 10970, doi:10.1073/pnas.0812764106 (2009).
- 689 10 Willcox, G. & Stordeur, D. Large-scale cereal processing before domestication during the  
690 tenth millennium cal BC in northern Syria. *Antiquity* **86**, 99-114 (2012).
- 691 11 Colledge, S. in *The origins of agriculture and crop domestication* (eds A.B. Damania, J.  
692 Valkoun, G. Willcox, & C.O. Qualset) 121–131 (ICARDA, 1998).
- 693 12 Hillman, G. C., Hedges, R., Moore, A. M. T., Colledge, S. & Pettitt, P. New evidence of  
694 Lateglacial cereal cultivation at Abu Hureyra on the Euphrates. *The Holocene* **11**, 383-393,  
695 doi:10.1191/095968301678302823 (2001).
- 696 13 Willcox, G. Searching for the origins of arable weeds in the Near East. *Vegetation History and*  
697 *Archaeobotany* **21**, 163-167, doi:10.1007/s00334-011-0307-1 (2012).
- 698 14 Harris, D. R. & Fuller, D. Q. in *Encyclopedia of global archaeology* (ed C Smith) 104-113  
699 (Springer, 2014).
- 700 15 Grime, J. P., Hodgson, J. G. & Hunt, R. *Comparative plant ecology: a functional approach to*  
701 *common British species*. (Springer, 2014).
- 702 16 Harlan, J. R., de Wet, J. M. J. & Price, E. G. Comparative evolution of cereals. *Evolution* **27**,  
703 311-325, doi:10.2307/2406971 (1973).
- 704 17 Fuller, D. Q. Contrasting Patterns in Crop Domestication and Domestication Rates: Recent  
705 Archaeobotanical Insights from the Old World. *Annals of Botany* **100**, 903-924,  
706 doi:10.1093/aob/mcm048 (2007).
- 707 18 Asouti, E. in *Neolithic Corporate Identities. Studies in Early Near Eastern Production,*  
708 *Subsistence and Environment 20 SENESE 20* (eds Marion Benz, H.G.K. Gebel, & Trevor  
709 Watkins) 21-53 (Ex oriente, 2017).
- 710 19 Harris, D. R. in *Foraging and farming: the evolution of plant exploitation* (eds David R Harris  
711 & G Hillman) 11-26 (Unwin Hyman, 1989).

- 712 20 Smith, B. D. Low-Level Food Production. *Journal of Archaeological Research* **9**, 1-43,  
713 doi:10.1023/a:1009436110049 (2001).
- 714 21 Rindos, D. *The origins of agriculture: An evolutionary perspective*. (Academic Press, 1984).
- 715 22 Weide, A. Towards a Socio-Economic Model for Southwest Asian Cereal Domestication.  
716 *Agronomy* **11**, 2432 (2021).
- 717 23 Hillman, G. C. & Davies, M. S. Measured Domestication Rates in Wild Wheats and Barley  
718 Under Primitive Cultivation, and Their Archaeological Implications. *Journal of World*  
719 *Prehistory* **4**, 157-222 (1990).
- 720 24 Kislev, M. E., Hartmann, A. & Weiss, E. Impetus for sowing and the beginning of agriculture:  
721 Ground collecting of Wild Cereals. *Proceedings of the National Academy of Sciences* **101**,  
722 2692-2695 (2004).
- 723 25 Weide, A. *et al.* The Association of Arable Weeds with Modern Wild Cereal Habitats:  
724 Implications for Reconstructing the Origins of Plant Cultivation in the Levant. *Environmental*  
725 *Archaeology*, 1-16, doi:10.1080/14614103.2021.1882715 (2021).
- 726 26 Zohary, M. The segetal plant communities of Palestine. *Vegetatio* **2**, 387-411 (1950).
- 727 27 Abbo, S., Lev-Yadun, S. & Gopher, A. Plant Domestication and Crop Evolution in the Near  
728 East: On Events and Processes. *Critical Reviews in Plant Sciences* **31**, 241-257,  
729 doi:10.1080/07352689.2011.645428 (2012).
- 730 28 Wood, D. & Lenné, J. M. A natural adaptive syndrome as a model for the origins of cereal  
731 agriculture. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20180277,  
732 doi:doi:10.1098/rspb.2018.0277 (2018).
- 733 29 Bogaard, A., Palmer, C., Jones, G., Charles, M. & Hodgson, J. G. A FIBS Approach to the Use of  
734 Weed Ecology for the Archaeobotanical Recognition of Crop Rotation Regimes. *Journal of*  
735 *Archaeological Science* **26**, 1211-1224, doi:<https://doi.org/10.1006/jasc.1998.0364> (1999).
- 736 30 Jones, G., Bogaard, A., Charles, M. & Hodgson, J. G. Distinguishing the Effects of Agricultural  
737 Practices Relating to Fertility and Disturbance: a Functional Ecological Approach in  
738 Archaeobotany. *Journal of Archaeological Science* **27**, 1073-1084,  
739 doi:<https://doi.org/10.1006/jasc.1999.0543> (2000).
- 740 31 Díaz, S. *et al.* The global spectrum of plant form and function. *Nature* **529**, 167-171,  
741 doi:10.1038/nature16489 (2016).
- 742 32 Garnier, E., Navas, M.-L. & Grigulis, K. *Plant functional diversity: organism traits, community*  
743 *structure, and ecosystem properties*. (Oxford University Press, 2016).
- 744 33 Bogaard, A. *Neolithic Farming in Central Europe*. (Routledge, 2004).
- 745 34 Bogaard, A. *et al.* From Traditional Farming in Morocco to Early Urban Agroecology in  
746 Northern Mesopotamia: Combining Present-day Arable Weed Surveys and Crop Isotope  
747 Analysis to Reconstruct Past Agrosystems in (Semi-)arid Regions. *Environmental Archaeology*  
748 **23**, 303-322, doi:<https://doi.org/10.1080/14614103.2016.1261217> (2018).
- 749 35 Hamerow, H. *et al.* An Integrated Bioarchaeological Approach to the Medieval 'Agricultural  
750 Revolution': A Case Study from Stafford, England, c. ad 800–1200. *European Journal of*  
751 *Archaeology* **23**, 585-609, doi:10.1017/eea.2020.6 (2020).
- 752 36 Green, L., Charles, M. & Bogaard, A. Exploring the agroecology of Neolithic Çatalhöyük,  
753 Central Anatolia: An archaeobotanical approach to agricultural intensity based on functional  
754 ecological analysis of arable weed flora. *Paléorient* **44**, 29-44 (2018).
- 755 37 Green, L. *Assessing the nature of early farming in Neolithic western Asia: a functional*  
756 *ecological approach to emerging arable weeds*, University of Oxford, (2017).
- 757 38 Atran, S. Hamula Organisation and Masha'a Tenure in Palestine. *Man* **21**, 271-295,  
758 doi:10.2307/2803160 (1986).
- 759 39 Palmer, C. 'Following the plough': the Agricultural Environment of Northern Jordan. *Levant*  
760 **30**, 129-165, doi:10.1179/lev.1998.30.1.129 (1998).
- 761 40 Noy-Meir, I., Gutman, M. & Kaplan, Y. Responses of Mediterranean Grassland Plants to  
762 Grazing and Protection. *Journal of Ecology* **77**, 290-310, doi:10.2307/2260930 (1989).

- 763 41 Noy-Meir, I. The effect of grazing on the abundance of wild wheat, barley and oat in Israel.  
764 *Biological Conservation* **51**, 299-310, doi:[https://doi.org/10.1016/0006-3207\(90\)90115-6](https://doi.org/10.1016/0006-3207(90)90115-6)  
765 (1990).
- 766 42 Håkansson, S. in *Biology and ecology of weeds* (eds W. Holzner & M. Numata) 123-135  
767 (Springer Netherlands, 1982).
- 768 43 Charles, M., Bogaard, A., Jones, G., Hodgson, J. & Halstead, P. Towards the archaeobotanical  
769 identification of intensive cereal cultivation: present-day ecological investigation in the  
770 mountains of Asturias, northwest Spain. *Vegetation History and Archaeobotany* **11**, 133-142  
771 (2002).
- 772 44 Hartmann-Shenkman, A., Kislev, M. E., Galili, E., Melamed, Y. & Weiss, E. Invading a new  
773 niche: obligatory weeds at Neolithic Atlit-Yam, Israel. *Vegetation History and Archaeobotany*  
774 **24**, 9-18, doi:10.1007/s00334-014-0498-3 (2015).
- 775 45 Kuijt, I. in *The Neolithic Demographic Transition and its Consequences* (eds Jean-Pierre  
776 Bocquet-Appel & Ofer Bar-Yosef) 287-313 (Springer Netherlands, 2008).
- 777 46 Bogaard, A. *et al.* Private pantries and celebrated surplus: storing and sharing food at  
778 Neolithic Çatalhöyük, Central Anatolia. *Antiquity* **83**, 649-668,  
779 doi:10.1017/S0003598X00098896 (2009).
- 780 47 Jones, G. *et al.* The origins of agriculture: Intentions and consequences. *Journal of*  
781 *Archaeological Science* **125**, 105290, doi:<https://doi.org/10.1016/j.jas.2020.105290> (2021).
- 782 48 Weiss, E., Kislev, M. E., Simchoni, O., Nadel, D. & Tschauer, H. Plant-food preparation area  
783 on an Upper Paleolithic brush hut floor at Ohalo II, Israel. *Journal of Archaeological Science*  
784 **35**, 2400-2414, doi:<http://dx.doi.org/10.1016/j.jas.2008.03.012> (2008).
- 785 49 Kluyver, T. A., Charles, M., Jones, G., Rees, M. & Osborne, C. P. Did greater burial depth  
786 increase the seed size of domesticated legumes? *Journal of Experimental Botany* **64**, 4101-  
787 4108, doi:10.1093/jxb/ert304 (2013).
- 788 50 Preece, C., Jones, G., Rees, M. & Osborne, C. P. Fertile Crescent crop progenitors gained a  
789 competitive advantage from large seedlings. *Ecology and Evolution* **11**, 3300-3312,  
790 doi:<https://doi.org/10.1002/ece3.7282> (2021).
- 791 51 Halstead, P. *Two oxen ahead: pre-mechanized farming in the Mediterranean*. (John Wiley &  
792 Sons, 2014).
- 793 52 Anderson, P. C. in *The Origins of Agriculture and Crop Domestication* (eds A.B. Damania, J.  
794 Valkoun, G. Willcox, & C.O. Qualset) 145-159 (ICARDA, 1998).
- 795 53 Mercuri, A. M., Fornaciari, R., Gallinaro, M., Vanin, S. & di Lernia, S. Plant behaviour from  
796 human imprints and the cultivation of wild cereals in Holocene Sahara. *Nature Plants* **4**, 71-  
797 81, doi:10.1038/s41477-017-0098-1 (2018).
- 798 54 Spengler, R. N. & Mueller, N. G. Grazing animals drove domestication of grain crops. *Nature*  
799 *Plants* **5**, 656-662, doi:10.1038/s41477-019-0470-4 (2019).
- 800 55 Smith, B. D. General patterns of niche construction and the management of 'wild' plant and  
801 animal resources by small-scale pre-industrial societies. *Philosophical Transactions of the*  
802 *Royal Society of London B: Biological Sciences* **366**, 836-848 (2011).
- 803 56 Bogaard, A. *et al.* Reconsidering domestication from a process archaeology perspective.  
804 *World Archaeology*, doi:10.1080/00438243.2021.1954990 (2021).
- 805 57 Coqueugniot, E. in *Espace naturel, espace habité en Syrie du Nord (10e - 2e millénaires av. J.-*  
806 *C.)* (eds M Fortin & O Aurenche) 109-114 (Maison de l'Orient et de la Méditerranée Jean  
807 Pouilloux, 1998).
- 808 58 Douché, C. *Émergence et développement des sociétés agricoles au Néolithique acéramique*  
809 *(Xe-VIIIe millénaires av. n. ère) étude archéobotanique de Dja'de El-Mughara et Tell Aswad,*  
810 *Syrie*. (Unpublished PhD thesis, 2018).
- 811 59 Noy, T. Gilgal I : A Pre-Pottery Neolithic site, Israel. The 1985-1987 seasons. *Paléorient*, 11-18  
812 (1989).

813 60 Bar-Yosef, O. & Gopher, A. in *An early Neolithic village in the Jordan valley* (eds Ofer Bar-  
814 Yosef & Avi Gopher) 41-69 (Peabody Museum of Archaeology and Ethnology, Harvard  
815 University, 1997).

816 61 Wright, K. I. The Social Origins of Cooking and Dining in Early Villages of Western Asia.  
817 *Proceedings of the Prehistoric Society* **66**, 89-121, doi:10.1017/S0079497X0000178X (2000).

818 62 Finlayson, B. Egalitarian societies and the earliest Neolithic of Southwest Asia. *Prehistoric  
819 Archaeology Journal of Interdisciplinary Studies* **3**, 27-43 (2020).

820 63 Bowles, S. & Choi, J.-K. The Neolithic Agricultural Revolution and the Origins of Private  
821 Property. *Journal of Political Economy* **127**, 2186-2228, doi:10.1086/701789 (2019).

822 64 Kuijt, I. The Neolithic refrigerator on a Friday night: How many people are coming to dinner  
823 and just what should I do with the slimy veggies in the back of the fridge? *Environmental  
824 Archaeology* **20**, 321-336, doi:10.1179/1749631415Y.0000000003 (2015).

825 65 Danin, A. Flora and vegetation of Israel and adjacent areas. *The zoogeography of Israel* **30**,  
826 251-276 (1988).

827 66 Jones, G., Bogaard, A., Halstead, P., Charles, M. & Smith, H. Identifying the Intensity of Crop  
828 Husbandry Practices on the Basis of Weed Floras. *The Annual of the British School at Athens*  
829 **94**, 167-189 (1999).

830 67 Sternberg, M., Gutman, M., Perevolotsky, A., Ungar, E. D. & Kigel, J. Vegetation response to  
831 grazing management in a Mediterranean herbaceous community: a functional group  
832 approach. *Journal of Applied Ecology* **37**, 224-237, doi:10.1046/j.1365-2664.2000.00491.x  
833 (2000).

834 68 Sternberg, M. *et al.* Testing the limits of resistance: a 19-year study of Mediterranean  
835 grassland response to grazing regimes. *Global Change Biology* **21**, 1939-1950,  
836 doi:10.1111/gcb.12866 (2015).

837 69 Caley, A. *et al.* High-intensity thinning treatments in mature *Pinus halepensis* plantations  
838 experiencing prolonged drought. *European Journal of Forest Research* **135**, 551-563,  
839 doi:10.1007/s10342-016-0954-y (2016).

840 70 Osem, Y., Perevolotsky, A. & Kigel, J. Grazing effect on diversity of annual plant communities  
841 in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in  
842 primary productivity. *Journal of Ecology* **90**, 936-946, doi:10.1046/j.1365-2745.2002.00730.x  
843 (2002).

844 71 Temper, L. Creating facts on the ground: Agriculture in Israel and Palestine (1882-2000).  
845 *Historia agraria: Revista de agricultura e historia rural*, 75-110 (2009).

846 72 Dan, J., Yaalon, D., Koyumdjisky, H. & Raz, Z. The soil association map of Israel (1:1,000,000).  
847 *Israel Journal of Earth Sciences* **21**, 29-49 (1970).

848 73 Sans, F. X. & Masalles, R. M. Phenological patterns in an arable land weed community  
849 related to disturbance. *Weed Research* **35**, 321-332, doi:[https://doi.org/10.1111/j.1365-  
850 3180.1995.tb01627.x](https://doi.org/10.1111/j.1365-3180.1995.tb01627.x) (1995).

851 74 Zohary, M. & Feinbrun-Dothan, N. *Flora Palaestina*. Vol. 1-4 (The Israel Academy of Sciences  
852 and Humanities, 1966-1986).

853 75 Davis, P. *Flora of Turkey and the East Aegean Islands*. Vol. Vol. 1-10 (Edinburgh University  
854 Press, 1965-1988).

855 76 Mortimer, A. M. in *Weed Control Handbook: Principles* (eds RJ Hance & K Holly) 1-42  
856 (Blackwell, 1990).

857 77 Douché, C. & Willcox, G. New archaeobotanical data from the Early Neolithic sites of Dja'de  
858 el-Mughara and Tell Aswad (Syria): A comparison between the Northern and the Southern  
859 Levant. *Paléorient* **44**, 45-58 (2018).

860 78 Jones, G. The application of present-day cereal processing studies to charred  
861 archaeobotanical remains. *Circaea* **6**, 91-96 (1990).

862 79 Bogaard, A., Jones, G. & Charles, M. The impact of crop processing on the reconstruction of  
863 crop sowing time and cultivation intensity from archaeobotanical weed evidence.  
864 *Vegetation History and Archaeobotany* **14**, 505-509, doi:10.1007/s00334-005-0061-3 (2005).

865 80 Bogaard, A. *et al.* in *Humans and Landscapes of Çatalhöyük: Reports from the 2000–2008*  
866 *Seasons* (ed I Hodder) 93-128 (Cotsen Institute of Archaeology/British Institute at Ankara,  
867 2013).

868 81 Filipović, D. *Early farming in Central Anatolia: an archaeobotanical study of crop husbandry,*  
869 *animal diet and land use at Neolithic Çatalhöyük.* *BAR International Series 2667.* (2014).

870 82 Helmer, D., Gourichon, L., Monchot, H., Peters, J. & Saña Seguí, M. in *New methods and the*  
871 *first steps of mammal domestication* (eds Vigne Jean-Denis, Peters Joris, & Helmer Daniel)  
872 86-95 (Oxbow Books, 2005).

873 83 Charles, M. Fodder from dung: the recognition and interpretation of dung-derived plant  
874 material from archaeological sites. *Environmental Archaeology* **1**, 111-122 (1998).

875 84 Kislev, M. E. in *An early Neolithic village in the Jordan valley* (eds Ofer Bar-Yosef & Avi  
876 Gopher) 209-236 (Peabody Museum of Archaeology and Ethnology, Harvard University,  
877 1997).

878 85 Kislev, M. E., Hartmann, A. & Noy, T. in *Gilgal: excavations at early Neolithic sites in the*  
879 *lower Jordan Valley. The Excavations of Tamar Noy* (eds O. Bar-Yosef, A. Nigel Goring-  
880 Morris, & A Gopher) 251-257 (Oxbow Books, 2010).

881 86 Snir, A., Nadel, D. & Weiss, E. Plant-food preparation on two consecutive floors at Upper  
882 Paleolithic Ohalo II, Israel. *Journal of Archaeological Science* **53**, 61-71,  
883 doi:<http://dx.doi.org/10.1016/j.jas.2014.09.023> (2015).

884 87 Jones, G., Charles, M., Bogaard, A. & Hodgson, J. Crops and weeds: the role of weed  
885 functional ecology in the identification of crop husbandry methods. *Journal of*  
886 *Archaeological Science* **37**, 70-77, doi:<https://doi.org/10.1016/j.jas.2009.08.017> (2010).

887 88 Šmilauer, P. & Lepš, J. *Multivariate analysis of ecological data using CANOCO 5.* (Cambridge  
888 University Press, 2014).

889 89 Galili, E. *et al.* Atlit-Yam: A Prehistoric Site on the Sea Floor off the Israeli Coast. *Journal of*  
890 *Field Archaeology* **20**, 133-157, doi:10.1179/jfa.1993.20.2.133 (1993).

891 90 Brenet, M., Sanchez-Priego, J. & Ibáñez-Estévez, J. J. in *Préhistoire et approche*  
892 *expérimentale* (eds L Bourguignon, I Ortega, & MC Frère-Sautot) 121-164 (éditions  
893 monique mergoil, 2001).

894 91 Bar-Yosef, O., Gopher, A., Goring-Morris, A. N. & Kozłowski, S. K. in *Gilgal. Early Neolithic*  
895 *Occupations in the Lower Jordan Valley: The Excavations of Tamar Noy* (eds O Bar-Yosef, A  
896 Gopher, AN Goring-Morris, & S Kozłowski) 11-26 (Oxbow Books, 2010).

897

