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

2 **Asia**

3

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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 record¹⁻³.
45 Snir *et al.*⁴ 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^{1,5}, increased grain sizes⁶⁻⁸, the presence of substantial storage
49 facilities^{9,10}, and the occurrence of crop progenitors outside of their natural distribution range¹. The
50 most direct evidence to suggest wild plant cultivation is, however, based on genera that include ara-
51 ble weed species^{1,4,7,8,11-13}. 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 tillage¹¹⁻¹³,
54 which generally feature as the defining aspects of cultivation as a subsistence practice¹⁴. 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 wildfires¹⁵. 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^{16,17}. 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 CO₂ during the Early Holocene^{1,18},
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^{5,10-12,17}. 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 disturbance¹⁹⁻²¹. 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^{17,19,22}.

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^{1,11,18}. 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. Davies²³, 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 Holocene³.
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^{1,17,23,24}. All these strategies
91 would maintain high proportions of shattering spikelets in the managed populations, suppressing
92 selection for non-shattering phenotypes. Alternatively, Asouti¹⁸ 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 ears³,
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.²⁵ 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 progenitors²⁶. 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^{25,27,28}. 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 anomalous²³. 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^{29,30}.

114

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

116 Plant functional traits occur in limited sets of combinations globally³¹ and can be used to assess, for
117 example, how ecological parameters affect species distribution and determine community
118 assembly³². 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^{30,33-36}. 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^{33,37}. 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 time³⁶.
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^{26,38}. 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')³⁹. 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^{40,41}. 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^{29,30}, 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 disturbance¹⁵. Similarly, perennials that rapidly regenerate from root and rhizome fragments
155 perform well under conditions of high mechanical disturbance, which even facilitates their growth⁴².
156 These traits were related to conditions of high mechanical disturbance in different climatic and eco-

157 logical settings, including England³⁵, Greece³⁰, Spain⁴³, and Morocco³⁴, demonstrating that they func-
158 tion independently from local environmental conditions and are applicable to archaeological con-
159 texts³³⁻³⁵.

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^{1,4,5,9,10,13}. 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)^{36,44}. 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^{45,46}. 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^{28,47}, 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.²⁵ 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^{25,26}. 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*)⁴⁸. The selection of potential arable weeds used by Snir *et al.*⁴ 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.*³⁶ 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 site⁶ 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 seeds⁴⁹. Large-seeded phenotypes have strong competitive advantages under conditions of
275 high interspecific competition due to their higher germination success and larger plant size⁵⁰. 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 habitations⁵⁰.

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^{14,51}.

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 Lenné²⁸
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^{47,50}. 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 ethnographically²⁰. 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 cereals²⁵.

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 tillage²³. 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 stands⁵². 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 world⁵³⁻⁵⁵, highlight-
327 ing that emerging domestication processes are generally grounded in ecological collaborations be-
328 tween humans and other organisms^{21,56}.

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^{14,17,19}. 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^{10,13}. 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)¹⁰. 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)^{57,58}.
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 element¹⁰. 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)^{5,59}, and possible clay storage silos with diameters between 1–3m at Netiv
352 Hagdud (Fig. 3g)⁶⁰. 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^{8,9}. These silos, together with the location of food processing and preparation
356 facilities inside and outside of residential structures⁶¹, likewise suggest a communal organisation of
357 cereal exploitation, storage, processing, and consumption activities at key PDC sites in the southern
358 Levant⁹. 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 individuality⁶². 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 investments⁶³.
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^{46,61,64}. 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)^{36,46}. 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 regions⁶⁵ 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.*²⁵). 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.*⁶⁶ and adjusted by Bogaard *et al.*³⁴. In each
386 plot we recorded all species in five 1m² 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⁻¹ year⁻¹). The vegetation was sampled along four and five transects, respectively, using the
397 step-point method⁶⁷. It has been acknowledged that this method misses rare species and can under-
398 estimate species richness⁶⁸, 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* plantation⁶⁹. 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 m² 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–December⁷⁰. 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 environments²⁶
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 100m² 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 periods³⁸. 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^{39,51}. 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^{26,39}. 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 period⁷¹, 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")⁷².
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^{29,30,35}.

440 Flowering duration is positively associated with conditions of high and unpredictable disturbance
441 such as soil tillage¹⁵. 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 early⁷³. 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*⁷⁴ and *Flora of*
450 *Turkey*⁷⁵. 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^{42,76}. 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 disturbance¹⁵. Large terminal tubers and vertical tap roots can be classified as stationary sensu
459 Håkansson⁴² 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^{74,75}.

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 Green³⁷ 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 contexts³⁶,
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.*¹ and Douché⁷⁷. The status of non-
481 crop taxa as weed contaminants was confirmed via a crop processing analysis detailed in^{37,78}, 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 species⁷⁹. 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 Green³⁷). Dung-derived taxa identified through previous taphonomic
491 analyses were excluded from the samples of Çatalhöyük^{80,81}. Despite evidence for cattle manage-

492 ment and morphological changes at Dja'de⁸², 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^{37,83}.

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)⁴⁴. 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, Kislev⁸⁴ 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. *dicoccooides*, *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 grains⁸⁵. 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. *dicoccooides*, *Lens* sp.).

509 The analysed assemblage from Ohalo II represents accumulations of plant remains on two consecu-
510 tive floors of hut 1^{48,86}. 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. *dicoccooides*, *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*)^{48,86}, and (2) the
518 potential weed assemblage selected by Snir et al.⁴.

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^{43,87}. The floristic composition of individual sites and their rela-
524 tionship to each other was explored via correspondence analysis (CA) using CANOCO 5⁸⁸. 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.²⁵. As sample distribution was potentially biased by the arch-effect, we detrended the ordination
528 model by segments using a detrended correspondence analysis (DCA)⁸⁸.

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

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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

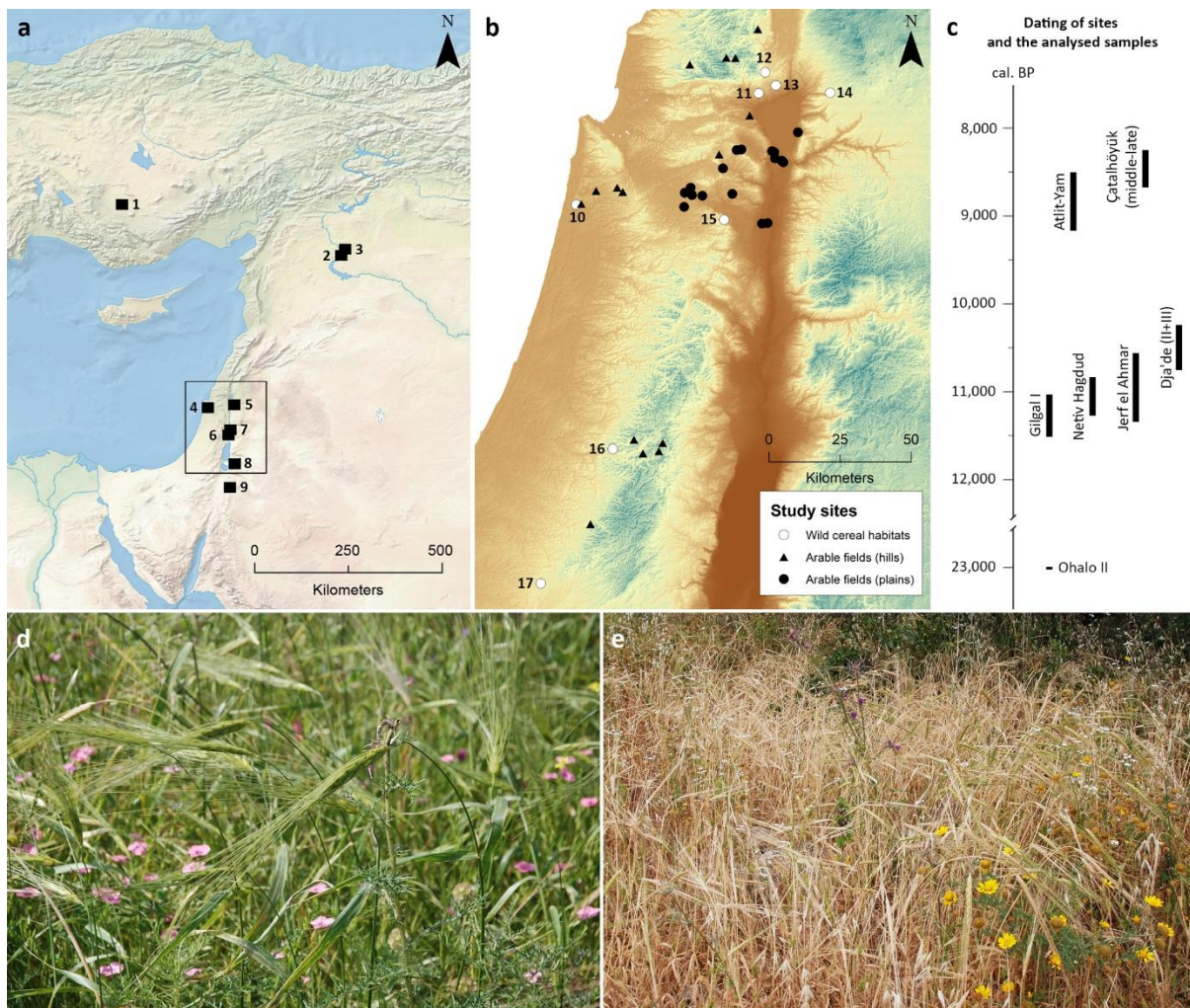
562 **Competing Interests Statement**

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

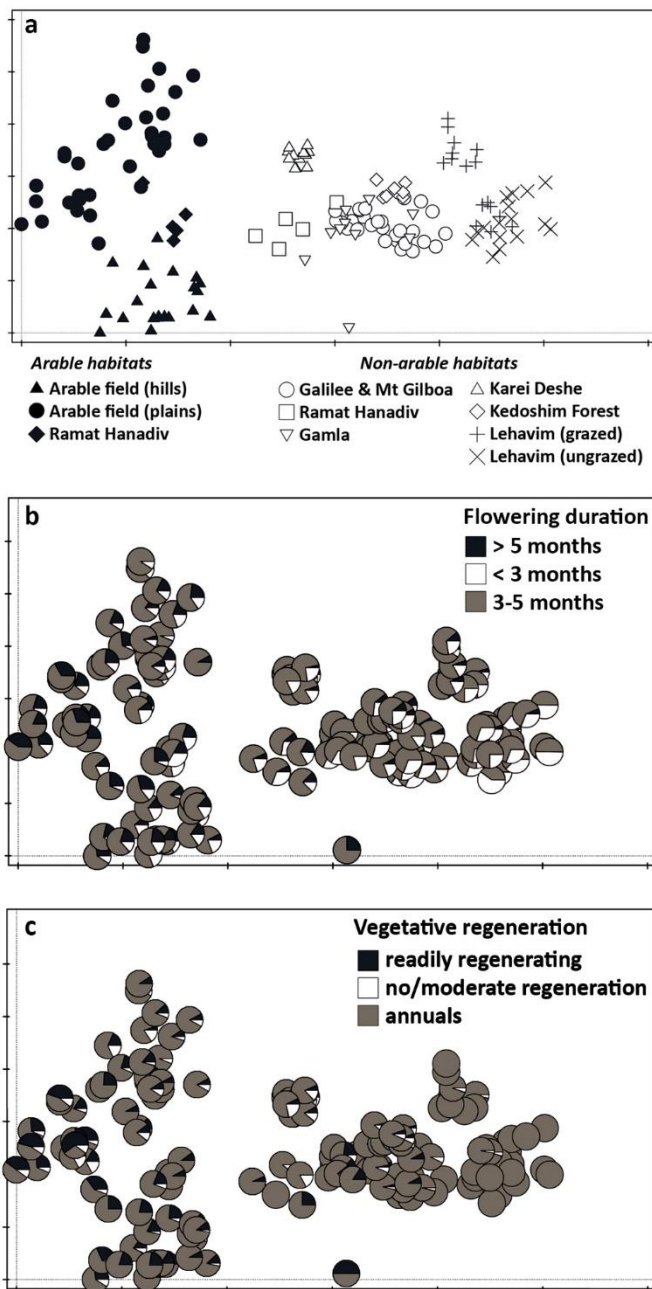


Fig. 2 a) DCA plot of samples from modern arable and non-arable habitats; **b)** distribution of long- and short-flowering species among the surveyed habitats; **c)** distribution of species after their capacity to regenerate vegetatively under conditions of high disturbance.

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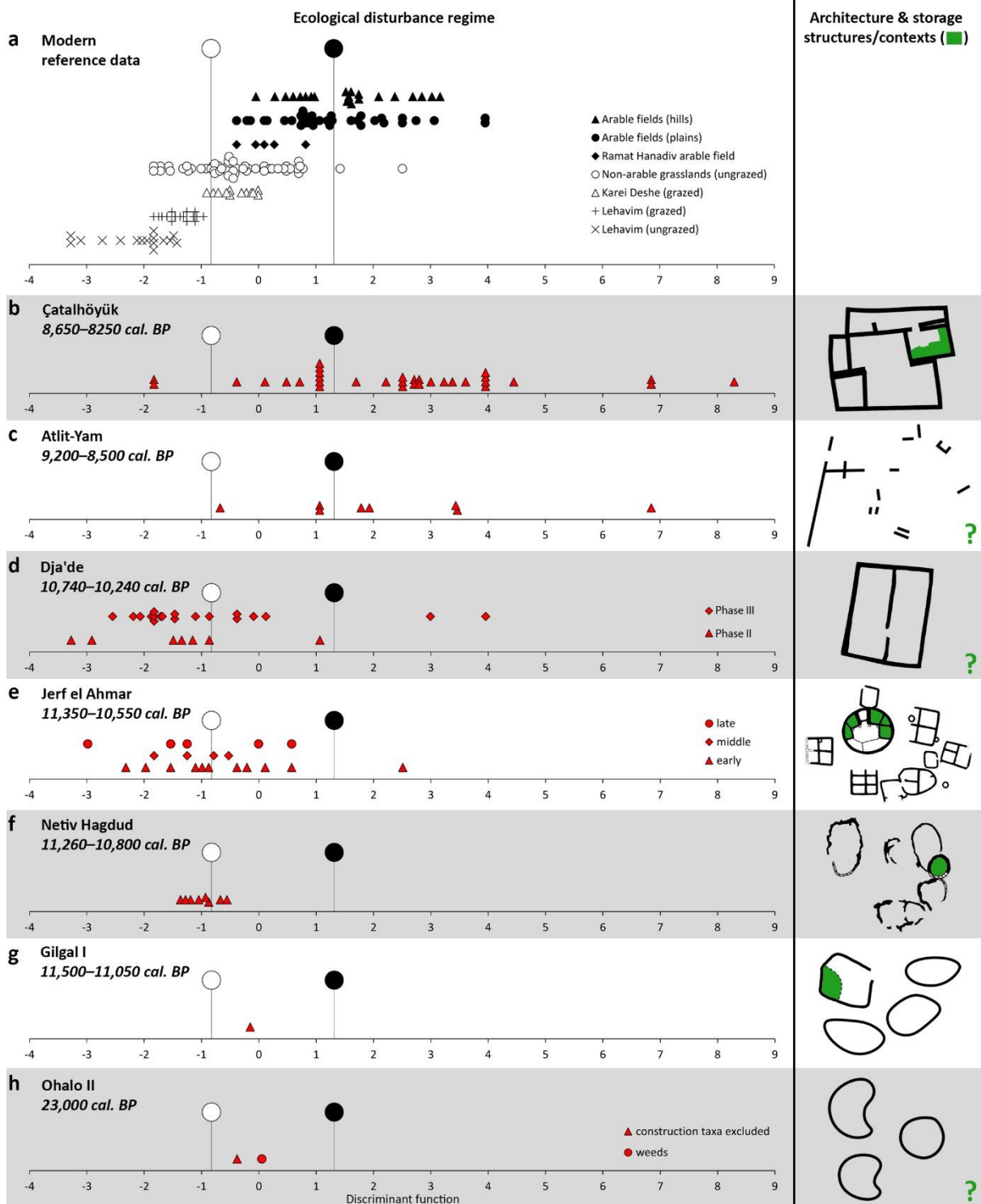
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607 **Fig. 3** Discriminant function extracted from the discriminant analysis using only flowering duration as
 608 a discriminating variable; the archaeobotanical samples (in red) are correlated with an example of
 609 the typical residential architecture (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.⁴⁶; **c**) samples from Atlit-Yam and parts of the settle-
614 ment plan (storage mode unclear), redrawn from Galili et al.⁸⁹; **d**) samples from Dja'de with building
615 EA6 (phase II, storage mode unclear), redrawn from Douché⁵⁸; **e**) samples from Jerf el Ahmar with
616 architecture from level II/W (late phase) including the communal building EA30 with storage bins,
617 redrawn from Brenet et al.⁹⁰; **f**) samples from Netiv Hagdud and parts of the settlement plan with a
618 potential free-standing storage silo, redrawn from Bar-Yosef and Gopher⁶⁰; **g**) sample from Gilgal I
619 with parts of the settlement plan, the cereal hoard derives from structure 11, redrawn from Bar-
620 Yosef et al.⁹¹; **h**) samples from Ohalo II with parts of the settlement plan (arrangement of huts modi-
621 fied, storage mode unclear), redrawn from Weiss et al.⁴⁸.

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

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

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

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

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

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

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

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