

The plant trait flowering duration can identify prehistoric agricultural disturbance

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Weide et al. developed a functional ecological model that distinguishes Levantine grasslands from local arable fields along a function of increasing soil disturbance¹. In applying the model to a series of Late Pleistocene and Early Holocene sites, we argued that what has been referred to as ‘pre-domestication cultivation’^{2,3} cannot be equated with the origins of arable farming in southwest Asia. In his critique, Willcox places doubt on several methodological aspects of the study, including the taphonomic analyses, the identification of charred seeds to ecologically relevant taxonomic levels, and the suitability of flowering duration to inform about past disturbance conditions. Here we reply to his critique and show that the disturbance model is statistically robust and maintains all trends in a re-analysis that excludes species which Willcox identifies as non-weeds.

Selection of samples and species

The archaeobotanical assemblages analysed by Weide et al. derive from crop storage contexts (Çatalhöyük) and mixed deposits (all other sites). We followed the standard procedure for selecting samples for an ecological analysis of crop growing conditions that is explained in detail in the original publication and elsewhere^{1,4-10}. The taxa used by Weide et al. for the ecological analyses were reported by Green¹¹ (tables 9.26, 9.29, and 9.34) and are openly accessible via the Oxford Research Archive: <https://ora.ox.ac.uk/objects/uuid:09a905ab-e375-4d45-bc27-d12cc21e9451>.

Independently from the taphonomic analyses, Willcox criticises the inclusion of some species in the ecological analyses. He argues that the species *Androsace maxima* and *Tribulus terrestris* are unlikely to have grown among wild cereals or in arable fields, despite both species being reported as arable weeds in the study region¹². *Bolboschoenus glaucus* is a freshwater plant that grows in dense stands along rivers or in moist depressions¹³, which Willcox takes as evidence against its status as a potential weed in dry-farmed cereal fields or early Holocene wild cereal habitats. However, the species is reported to perform well in summer-dry habitats and occurs as a weed in cereal fields along the Euphrates^{13,14}. Its association with wild cereals in archaeobotanical samples from Jerf el Ahmar and Dja'de may even hint towards the exploitation of cereals that grew near the Euphrates floodplain, although *B. glaucus* nutlets are not very frequent among the analysed samples from both sites (3 and 1 sample, respectively). However, based on their present-day ecology, we consider these three taxa as possible Neolithic cereal weeds.

Flowering duration as a predictor of past disturbance conditions

As Willcox only refers to one of our functional ecological models, we want to emphasise that we generated two models: one based on vegetative regeneration plus flowering duration, and one based on flowering duration only. As explained in detail in the original article, both models reach comparable reclassification scores for the modern habitats (90.2 versus 86.7%) and our conclusions are based on both models.

As Willcox rightly points out, plasticity in flowering phenology is related to geographically and temporally variable environmental factors. This argumentation is irrelevant to our discussion as it ignores

that functional ecological analyses are based on a species' ecological *potential* and not its phenotypical plasticity¹⁵. He further argues that flowering duration obtained from modern Floras cannot be applied to early Holocene datasets, while speculating that flowering duration would have changed over time in response to changing climatic conditions and in adaptation to emerging arable environments.

Instead of mirroring climatic conditions, flowering duration primarily reflects a species' regenerative strategy that is closely linked to its functional traits¹⁵⁻¹⁸. Crucially, flowering duration is positively correlated with a species' potential to grow under conditions of high and unpredictable disturbance^{19,20}. Most arable weeds also grow outside of fields and are generally classified as ruderals according to Grime's CSR model²¹. Their longer average flowering duration is thus a general adaptation to disturbed habitats and we are not aware of datasets showing that long flowering duration primarily evolved under cultivation. The ruderals that entered arable habitats since the early Holocene were likely pre-adapted to high and unpredictable disturbance through their functional architecture, including early and prolonged flowering, and benefitted from the human-driven spread of such habitats.

Long-term phenological studies show that onset of flowering is on average only 2-6 days earlier per 1 °C temperature increase^{22,23}. Species responses to changing climatic conditions are variable, where an earlier onset of flowering does not automatically translate into longer flowering periods^{18,24}. These data show that even if many plants would flower earlier in response to a warmer and wetter early Holocene climate²⁵, the magnitude of change would be far too small to mimic a switch in ecological strategies deduced from flowering duration.

Taxonomic identifications and the statistical robustness of the ecological model

Willcox questions some taxonomic identifications, including the merging of species for the discriminant analysis. A first identification he doubts is *Polygonum aviculare*. This morphotype was identified based on morphological criteria¹¹ and is often referred to as *P. aviculare* agg., which also includes *P. arenastrum* and *P. mesembrium*²⁶ (see also Filipovic²⁷ for the identification at Çatalhöyük). However, flowering duration given by the Flora of Turkey for *P. aviculare* (5 months) does not diverge much from the average flowering duration of all three taxa (4.3 months) and such small differences do, as we show below, not affect the results of the disturbance model. Moreover, Willcox doubts the identification of *P. aviculare* agg. based on its unknown past distribution and modern habitat preferences. However, its identification at Jerf el Ahmar and Dja'de (based on detailed morphological analysis) provides direct evidence for this taxon's early Holocene distribution along the middle Euphrates¹¹. That *P. aviculare* agg. was part of early west Asian weed floras is further supported by its frequent occurrence in crop stores at Çatalhöyük²⁸.

A further criticism concerns the identified *Bromus* and *Adonis* species. For the first taxon, Green¹¹ developed a detailed and accessible species identification key. Where species were merged for the functional ecological analysis, the identification reached a taxonomic level sufficient for attributing a trait value as explained in our article. For example, the two *Adonis* species that should not be merged according to Willcox are *A. annua* and *A. aestivalis*¹¹. The species have flowering durations of 3 and 2 months, respectively, based on the Flora Palaestina, resulting in an applied average trait value of 2.5. A divergence of 0.5 months has no significant effect on the statistical output of the DA because even the exclusion of several species from the archaeological datasets does not affect the overall trends as demonstrated below.

To show that the trends observed among the archaeobotanical datasets are statistically robust and do not depend on the inclusion of individual species identified by Willcox as non-weeds, we include here a discriminant analysis (DA) for Çatalhöyük, Jerf el Ahmar, and Dja'de excluding these taxa (Table 1).

Figure 1 shows that the spectrum of discriminant values, reflecting average flowering duration of species associated with wild cereals and pulses, remains almost unchanged, confirming the results of the original analyses. Taking all taphonomic, ecological, taxonomic, and statistical considerations together, we can reject Willcox' argument that our analyses are unreliable due to the selection of certain weed taxa and the use of flowering duration as a disturbance-related plant trait.

Author Contributions

A.W. performed the data re-analysis and led the writing process. All authors contributed to the ideas and the final response.

Competing Interests Statement

We have no competing interests.

Table 1 | Taxa selected for the original and re-analysed discriminant analyses

Site	<i>n</i> species included in DA		Excluded in re-analysis
	Weide et al. ¹	Re-analysis	
Çatalhöyük	19	17	<i>Androsace maxima</i> <i>Phragmites australis</i>
Dja'de	17	13	<i>Androsace maxima</i> <i>Bolboschoenus glaucus</i> <i>Polygonum aviculare</i> <i>Tribulus terrestris</i>
Jerf el Ahmar	17	13	<i>Androsace maxima</i> <i>Bolboschoenus glaucus</i> <i>Polygonum aviculare</i> <i>Tribulus terrestris</i>

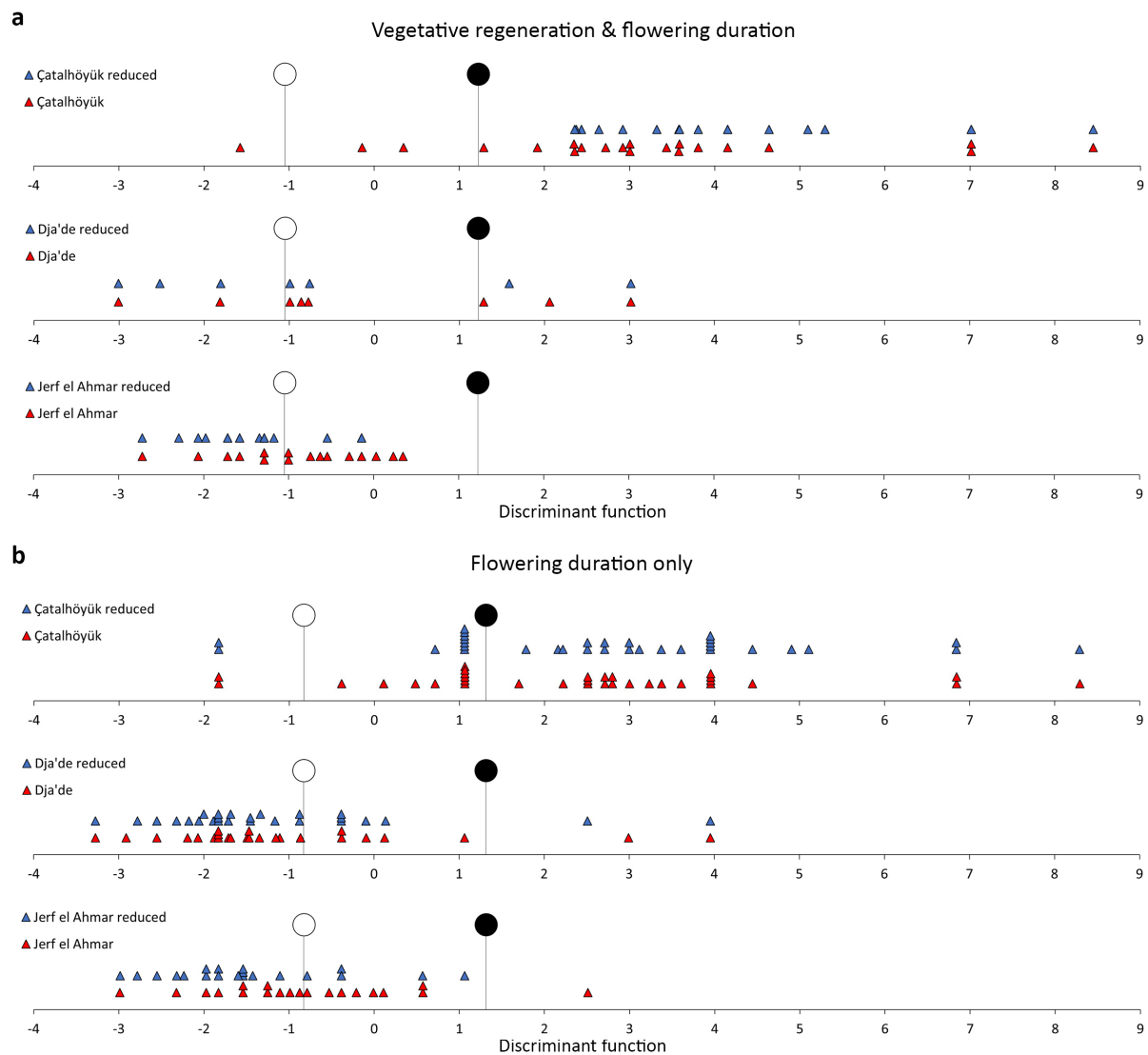


Fig. 1 | Comparison of the discriminant functions extracted for Çatalhöyük, Dja'de, and Jerf el Ahmar using different traits and species combinations. The archaeobotanical samples displayed in red represent the dataset published by Weide *et al.*¹, compared to the group centroids of the modern functional model (open circle = grasslands; closed circles = arable fields). Samples in blue represent a reduced dataset where species suggested to be non-weeds were excluded (see Table 1). **a**, Discriminant functions extracted from a DA using flowering duration and the ability of perennials to regenerate vegetatively. **b**, Discriminant functions extracted from a DA using only flowering duration as a discriminating variable.

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