Review

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A natural adaptive syndrome as a model for the origins of cereal agriculture

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A novel explanation of the origin of cereal agriculture is proposed, based on the ecology and adaptive morphology of wild cereals ancestral to our founder cereals (einkorn, emmer and barley). Wild cereals are unusually large-seeded. A natural evolutionary-ecological syndrome relates *l*arge seed, *a*wns and *m*onodominance (LAM). Awns bury attached seeds in the soil, protecting seed from fire; buried seed needs to be large to emerge on germination; large seeds, growing without competition from small-seeded plants, will produce monodominant vegetation. Climatic and edaphic instability at the Pleistocene–Holocene boundary would have provided an impetus for the spread of annual ruderal grasses. LAM grassland provided an obvious natural model for the origins of cereal agriculture. Subsequent field management would mimic the natural niche (MNN). The fact that monodominance is a long-standing character of the natural LAM syndrome validates cereal mono-cultures (now producing most of our food). An alternative explanation of crop domestication, by auditioning a great range of species for a human-constructed niche (NCT), is rejected.

1. Introduction

The domestication of a very limited range of wild grasses in the Fertile Crescent of Southwest Asia was a major feature of human cultural development. Yet attempts to provide a simple and fact-based explanation of the origins of agriculture are faltering. After more than 100 years, there are no easy answers to questions about domestication and agricultural origins [1]. Rather, there are still unresolved problems and little hope of agreement on any single explanation.

(a) 'Talking past each other in a crowded room'

The continuing problems can be exemplified by the results of three workshops, each bringing together specialists in agricultural origins for the purpose of reaching consensus. The *first workshop* in 2007 raised a concern that several contributions remain locked into conceptual frameworks that arose 20 or 30 years ago, and that there was a need to maintain an openness to new directions [2]. Tellingly, the subtitle of one contribution to the meeting was 'Talking past each other in a crowded room' [3]. The *second workshop*, in 2009, reported that they did not yet have a good grasp on the causes for the origins of agriculture, only a series of ideas and suggestions that do not quite resolve the problem [4]. The *third workshop*, a 'catalysis meeting' in 2011 [5], admitted that explaining the origins of agriculture is still one of the most contentious issues for social scientists, with a complex and unresolved situation in studies of crop domestication.

(b) The challenge

This continued lack of consensus [6], and even confusion over agricultural origins, justifies the need to continue to challenge existing models [7]. However, since the inconclusive results of the three workshops, a further layer of complexity has been added to origin of agriculture studies. Anthropologists are now promoting a view of domestication based on the emerging ideas of niche construction theory (NCT) involving cultural inheritance [8].

This review will heed a suggestion of two decades ago: that ecological research was the weak link in agricultural origins studies [9]. There is copious existing and still-growing evidence of the morphology, ecology and evolutionary behaviour of the wild cereals associated with the earliest domestication events in the Fertile Crescent. Using existing information a working hypothesis will be adopted, with an ecological base: 'A natural adaptive syndrome of three species of wild cereals was the model for the human management of the first cereals during domestication.'

This review focuses on the Fertile Crescent and surrounding regions, where by far the most research has been done and where the three founder cereals were located. There is an encyclopaedic coverage of these founder cereals, with distribution maps and correct naming (which we will use) [10]. The cereals are einkorn wheat (*Triticum monococcum* subsp. *monococcum*), emmer wheat (*Triticum turgidum* subsp. *dicoccum*) and barley (*Hordeum vulgare* subsp. *distichum*). The corresponding wild relatives are wild einkorn (*T. monococcum* subsp. *baeoticum*), wild emmer (*T. turgidum* subsp. *dicoccoides*) and wild barley (*H. vulgare* subsp. *spontaneum*). All three wild relatives are in the grass tribe Triticeae [11].

2. An adaptive syndrome in wild relatives of founder cereals

(a) Large seed in wild grasses

Cereals producing most of our food are annuals: their immediate wild ancestral species are annuals. By definition, year by year, the seed of annual species has to survive and germinate to ensure the future of the species: protection of seed is critical. A further striking feature of species ancestral to our first cereals is that they are large-seeded, unusually so for grasses—a characteristic that substantially pre-dates domestication. It has been claimed that the wild relatives of subsequent domesticates (wheat, maize and rice) were small-seeded [12]. As we found, this is not true: indeed, agricultural origins had already been linked to 'caryopsis gigantism', that is, very big seed [13].

It is notable that seeds of ancestors of the three founder cereals were already in the top 1% of all grass seed weights before domestication. An early review [14] showed that 32 of the 56 largest-seeded grasses in the world were to be found in the Fertile Crescent and adjacent areas, the region where the first three domesticated cereals appeared.

An analysis of large seed in grasses revealed its rarity. A search for grasses with seeds weighing more than 20 mg in the Kew database found only 40 species (2% of a total of 1997 grass species with recorded seed weights) [15]. Of these, there were 20 species of cereal wild relatives, including 10 *Aegilops* (wild relatives of wheat), 5 *Avena* (oats), 1 *Coix* (Job's tears), 1 *Hordeum* (barley), 1 *Oryza* (rice), 1 *Tripsacum* and 1 *Zea* (maize)—that is, only 1% of all grasses with recorded seed weights (table 1). Missed by the Kew seed database, which is still in preparation, were three direct ancestors of cereals that also have seeds weighing more than our cut-off of 20 mg: the crop progenitors *Triticum monococcum* subsp. *baeoticum* (ancestral to einkorn), *Triticum turgidum* subsp. *dicoccoides* (ancestral to emmer) and *Hordeum vulgare* subsp. *spontaneum* (ancestral to barley), with seed mass ranging from 21 mg in *T. monococcum* subsp. *baeoticum* to 28.9 mg in *H. vulgare* subsp. *spontaneum*. Seed mass was significantly larger in

Table 1. Grass and wild relative seed weights over 20 mg [15].

grass seed weights	species	%
grasses with known weights	1997	100.0
all grasses >20 mg	40	2.0
cereal relatives >20 mg	20	1.0

these three wild ancestral species than in six wild relatives never domesticated [16]. Thus the wild ancestors of einkorn, emmer and barley had unusually large seed before domestication, and long before human management.

(b) Seed-burying by awns

Any large seed, with food reserves to allow germination and seedling establishment, is an obvious food source for seed-eating animals and must have some mechanism for protection [17]. This concept led to a significant explanation as to how large seeds of tropical forest trees survive under entirely natural conditions [18]. It was found that large seeds of trees growing in species-poor stands were protected against seed-eating animals by high levels of toxins. The key question for the first domestication of cereals (einkorn, emmer and barley) is: 'How did annual wild cereals with unusually large seeds protect their seed from predation?' Apart from seed loss from seed-eating animals there is an additional requirement for seed protection in seasonally dry grassland, where grassland fires will destroy seed on the soil surface.

Wild ancestors of all three founder species—einkorn, emmer and barley—have seeds with attached awns. These awns are scabrous—that is, rough, with minute barbs pointing to the tip of the awn. Such awns are thought to be adaptations to insert the large, narrow seeds into the soil. This ability to penetrate the soil was described in an account of the flora of Palestine [19], which was partly based on an earlier account of awn movement in wild emmer, goat grass (*Aegilops*) and *Bromus* species [20]. With the warning that it had become routine to ascribe dispersal abilities to any appendages of seeds and fruits without examining their real function, a new non-dispersal mechanism—topochory—was described, functioning to forestall long-distance dispersal to ensure seeds stayed in the vicinity of their parent plant (where, of course, the environmental conditions were suitable for growth). One of the several mechanisms of topochory was 'trypanocarpy' (auger fruit), described as a diaspore equipped with a hygroscopic drilling apparatus or a sharply-pointed tip which enables it to penetrate the soil—examples given include wild species of *Hordeum*, *Aegilops*, *Bromus* and *Triticum*, all awned [19]. The seed-bearing structures in wild wheats and barley were described as specialized arrow-shaped dissemination units which very effectively insert the mature fruiting units into the soil [21].

The mechanism by which scabrous awns function is described as a 'botanical ratchet' to move seed over the soil surface during flexion of the awn, which then buries the seed [22,23] (characteristic of *Triticum* and *Hordeum*, including the wild relatives of einkorn, emmer and barley). For the two-seeded diaspore (dispersal unit) of wild emmer the two scabrous awns can converge and diverge under diurnal humidity changes and drive the seeds into the soil—well illustrated in

[24]. In addition to hygroscopic movements of awns caused by humidity changes, external mechanical force may be needed.

> ...awns are the visible constituent of a compound morphological syndrome, the burial syndrome, that has been established through changes in a suite of diaspore traits over evolutionary time... Active burial is driven by the presence of a hygroscopically active awn and aided by a long, pointed callus that firmly anchors the caryopsis in the ground. [25, p. 1176].

The widespread distribution of awns across the grass family shows they are not a result of human selection. While seed-burying structures attached to seeds are found elsewhere in plants, for example in *Erodium cicutarium* (fam. Geraniaceae) [26], they are rare.

Applying an electronic key INTKEY [27] to the electronic database of the botanical descriptions of all 11 313 grasses [28] it is possible to identify a group of 46 species using just four awn characters from a total list of 1063 characters. The four awn characters are: the fertile lemma is 1-awned; the awn is straight; it is scabrous; and it is greater than 80 mm in length. Remarkably, these 46 species include a wild relative of barley, and two wild wheats and three wild rices (and also five domesticated wheats and domesticated Asian rice), that is, 12 species of crops and relatives in all. Ancestors of two founder cereals (wild emmer and wild barley) are included but wild einkorn is not, having awns up to only 60 mm. The grouping of related characters of the awns of early cereals and their wild relatives is rare, being found in only 0.40% of 11 313 grass species. Clearly, the long awns of the lemmas in ancestral wild cereals are major, rare, but hitherto unrecognized characteristics of cereal domestication.

(c) Monodominant grassland

Large seeds lead to vegetation with low species richness, with, for example, monodominant *Mora oleifera* forest with very large, toxic seeds, and monodominant *Rhizophora* mangroves with large seedlings developed and held for protection on the tree before dispersal [18]. It was claimed that the existence of such forests falsifies the dogma that diversity is mandatory for ecosystem stability in highly equitable climates. Later research and modelling on tropical forest has confirmed the relationship of large seed and monodominance [29,30].

A pantheon of botanists has provided strong evidence of monodominant 'fields' of wild cereals [31,32] with stands of wild cereals developing as dense as sown cultivated fields when protected from livestock [33]. Zohary details extensive masses and 'wild fields' characteristic of two wild wheats: *Triticum monococcum* subsp. *baeoticum* (wild einkorn) and *Triticum turgidum* subsp. *dicoccoides* (wild emmer) [21]. Such wild wheats are found in primary habitats—that is, apparently undisturbed by humans. Similarly, wild barley was massively and continuously spread over primary habitats. Danin [34] has an excellent photograph of dense stands of wild barley. In the Near East, Harlan [35] noted that massive stands of wild wheats cover many square kilometres. For example, wild emmer is as abundant in the Upper Jordan Valley as the vast stands of wild einkorn in the north, from Palestine to southeastern Turkey, west to Anatolia and eastward to western Iran and north to the Caucasus [36].

Botanists have harvested these wild stands experimentally. Hillman reported that wild einkorn tends to form dense stands which when harvested give yields that often match those of cultivated wheats under traditional management [37]. For wild einkorn in southeastern Turkey, a family group, working over a three-week harvest season, could easily gather more grain than the family could consume in a year [36].

(d) LAM: a natural adaptive syndrome for wild relatives of cereal crops

This review suggests a hitherto unrecognized natural evolutionary-ecological syndrome in the three wild ancestors of the first cereals, which relates *l*arge seed, *a*wns and *m*onodominance (LAM).

— One evolutionary response of annual grasses needing to protect seed is to develop hygroscopic or ratchet *awns* to bury seed, preventing damage.
— Of necessity, to emerge from deep soil on germinating, seeds need to be *large*.
— Buried large seed, germinating in soils where unburied seed has been eaten by animals or destroyed by natural fires will form *monodominant* grassland.

Two of these existing natural features—unusually large seed and the ability to form monodominant vegetation—would have been attractive to seed gatherers and could explain why LAM-syndrome wild cereals were initially exploited as a source of food and were then eventually domesticated.

However, the large seed and monodominance of LAM-syndrome wild cereals are only part of a wider explanation of domestication. There is a need to consider two related issues:

— What were the ecological features of the environment to which LAM characters were adapted?
— Did the ecology of LAM-syndrome wild cereals influence human management before and after the first cultivation?

3. Ecological settings of LAM vegetation: environmental disturbance

This review suggests that LAM grassland is natural vegetation with a long adaptive relationship to local environmental conditions of stress and disturbance. Grasses can be unusually adapted to stress. A review of world grasses claimed that grasses are adaptable to saline, alkaline and seasonally waterlogged soils, and capable of forming edaphic grasslands in such environments; benefit from a fire regime that is lethal to many other plants; and have evolved and adapted to unstable or fluctuating environments, in particular, strongly seasonal rainfall regimes or the early stages of succession following disturbance [38].

How can certain grass species attain monodominance and even invasiveness? There has to be some selective factor of the local environment to which the monodominant species is uniquely adapted, to which other species are not adapted. Of necessity this selective environmental factor must be a form of stress, capable of filtering out non-adapted species. In Janzen's paper—relating tropical blackwater rivers to toxic seed of rainforest trees—the selective factor for species-poor vegetation (to the point of monodominance) was edaphic—a deficiency of soil nutrients [18]. This stress, acting on long-lived trees, cannot explain the origin of annual cereals. However, Janzen's insight linking monodominance and environmental stress is crucial to understanding the ecology

of the first wild cereals, all annuals: their ecology may help to understand subsequent domestication and field management.

Monodominance is found in perennial and annual grasses but is uncommon worldwide: a minority of all grasses (approx. 600 out of approx. 11 000 species) is documented as being ecologically dominant in grasslands going back to Late Miocene to Pliocene [39]. In this review emphasis is given to the mechanisms such as fire and disturbance responsible for monodominance in annual grasses including the first wild cereals.

(a) The impact of fire on annual grasses

As the three ancestral species of the first cereals are annuals, most of their life cycle is spent as dormant seed buried in the soil. As annuals, all three are entirely reliant on seed for their survival. The most probable evolutionary stress to which these annuals need to be adapted would be short-term disturbance. Disturbance is defined as mechanisms which limit the plant biomass by causing its partial or total destruction [40]. This review has already suggested that the selective factor in grassland inhabited by the wild relatives of cereals is fire and the adaptive response is the ability of these wild annual grasses to bury seed to protect it from dry-season fires. This ability has two evolutionary consequences: large seeds can produce seedlings emerging from greater soil depths [41]; and seedlings from large seeds can better compete with seedlings from small seeds. As fire will destroy surface seed of any size (as it will do so to woody vegetation), the resulting vegetation is monodominant grassland. There is evidence for this; for example, after grass fires, wild emmer cover increased in ungrazed grasslands, as the cover of perennials was reduced [42]. This removal of perennial and woody vegetation indicates fire pressure on surface seed and rules out seed predation by animals, which would not distinguish between the seed of annuals *versus* perennials.

There is copious evidence for grassland fire in Southwest Asia, a key area of agricultural origins. A review of fire in Mediterranean ecosystems concluded that annual and perennial grass 'fire-followers' are also able to escape high surface fire temperatures with the aid of torsion devices on seeds [43]. Fire regimes were implicated in the site-specific response of large-seeded wild emmer, wild barley and wild oat (*Avena sterilis*), which dominated herbaceous vegetation of 'parkforest' in Israel [44]. There is a distinctive association between the Mount Tabor oak (*Quercus ithaburensis*) and, between the trees, a rich annual large-seeded herbaceous vegetation dominated by wild emmer, wild barley and wild oat. As a result of frequent fire hazards these annual grasses out-compete tree seedlings which only survive in the rock mounds where annuals do not grow [44].

(b) Naturally disturbed soils and annual LAM-syndrome grasses

While seasonal fires can explain the need for buried, large seed in annual wild cereals, the annual habit alone could be of adaptive advantage in other naturally disturbed environments, for example, seasonally disturbed soils. Seasonally flooded rivers offer one source of disturbed soil for annual ruderals such as LAM grasses. The north and east of the Fertile Crescent are drained by the Tigris and Euphrates rivers, both with annual floods, leaving behind bare silt available for seeding. To the west

of the Fertile Crescent is an extension of the African Rift Valley following the African and Arabian plate boundary [45], characterized by tectonic activity and high relief, with the erosion of side valleys producing silt and gravel fans with flowing streams allowing gravity irrigation. There is ample evidence for disturbed ground in the Pleistocene of the Southern Levant: landforms took shape as a result of vulcanism, cycles of erosion and deposition, and changing sea levels—noted as a time of significant palaeoenvironmental dynamism [46].

Another edaphic factor to which grasses need to adapt is soil salinity—the higher the salinity, the fewer species adapted to it and the more monodominant the remaining vegetation. Salinity is relevant to the distribution of wild cereals, at least some of which, including wild emmer and wild barley, are salt tolerant [47]: indeed, more than half the wild species of the barley genus *Hordeum* occupy habitats that are saline [48].

A combination of salinity and flood disturbance can explain claims for the earliest pre-domestication cultivation, made for Ohalo II, an early Epipalaeolithic site, dated to around 21000 BCE on the shores of the Sea of Galilee. Its importance is from the quality and identification of plant remains and the presence of 'proto-weeds', claimed to indicate cultivation—the earliest record of such [49]. However, the recognition of the LAM syndrome allows an alternative explanation of the presence of 'proto-weeds' at Ohalo II: they are not weeds growing in human-made niches, as claimed, but are ruderals—that is, wild plants of naturally disturbed ground. Indeed, the presence of wild cereals can also be explained by the nature of the lakeshore environment, disturbed by changes in water level (sudden inundation of the Ohalo II site is the reason it was so well preserved) and saline soils. The majority of the Ohalo II grasses, namely alkaligrass (*Puccinellia convoluta*), brome (*Bromus pseudobrachystachys/tigridis*), Mediterranean barley, and seaside barley (*Hordeum marinum*), all derive from saline habitats [50]. The wild barley and emmer are LAM grasses and are awned, as are two other species recorded in the seed samples, *Bromus tigridis* and *Alopecurus utriculatus* [51]. Present saline soils in the Dead Sea Valley are populated by plant communities which are poor in species number and may even be monospecific [52]. Ohalo II grass species are not evidence of pre-domestication cultivation: rather, they are ecological specialists of disturbed or saline soils.

There is a sound ecological explanation of the relation between annual species and disturbance. In Grime's triangular representation of plant strategies, annual herbs are mainly restricted to severely disturbed habitats [40,53]. The ancestors of the three founder cereals are all annuals adapted to withstand disturbance—that is, they are ruderals, which have a life cycle described as 'adapted to exploit environments intermittently favourable for rapid plant growth' [40, p. 43]. However, there is no direct evidence for robust and widespread vegetation of wild cereals prior to their domestication. Supposition of their robustness must be based on their present-day ecology as monodominants in their native environments (reviewed above).

There is also indirect evidence from the expansion and extraordinary dominance of annual awned grasses introduced into North America. Examples include cheatgrass (*Bromus tectorum*), the dominant species on more than 40 million ha [54], and *Avena sterilis* (a wild relative of oats). They are encouraged, rather than controlled, by fire [55], and illustrate the robustness and powerful competitive ability of annual awned grasses under disturbance regimes.

This review suggests that a similar spread of wild cereals associated with the environmental disturbance around the Pleistocene/Holocene transition and later, explains their long-standing value as a source of food and their eventual domestication.

4. Climate change and the spread of LAM-syndrome grasses

The end of the Pleistocene, with a complex and changing physical environment coupled with unstable climate with marked seasonal aridity, resulted in the repeated creation and destruction of different habitats. Further, annuals probably were the plants most successful in unstable locations, such as ecotonal transitions between continental and Mediterranean climate, between forest and steppe, and locales where the greatest opportunities existed for colonization by invasive species [56].

The Younger Dryas climate event, described as the slide into aridity [57], was accepted as having had profound effects on vegetation. However, attempts to link the Younger Dryas to negative impacts on vegetation face a problem. The Younger Dryas was not a one-way climate change, but a swing: negative impacts, if any, would be followed by positive impacts a thousand or so years later. In these changing environmental conditions it is probable that LAM-syndrome grasses—with their ability to persist through disturbance, including fire—would have flourished.

The Younger Dryas was a significant arid phase in the Levant, exhibiting overall decreased precipitation and lowered lake levels and intensively dry and cool conditions for about 1300 years. This may have caused soil disturbance allowing ruderal LAM species to spread. In contrast, the end of the Younger Dryas was marked by higher water tables, terrace aggradations, and accumulation of colluvial, alluvial and spring deposits at several sites throughout the southern Levant, yet more possibilities of increased soil disturbance [58].

This review contends that annual wild relatives of the first cereals, evolved under natural disturbance, were able to spread as ruderals and eventually dominate disturbed conditions at the Pleistocene–Holocene boundary, in particular, the climate swings into and out of the Younger Dryas. But rather than being an incentive for cultivation, the climate changes and associated vegetation changes around the Pleistocene–Holocene boundary could have acted as a disincentive to cultivation. The long-standing reasoning of Harlan & Zohary addressed this [31, p. 1079]:

> Why should anyone cultivate a cereal where natural stands are as dense as a cultivated field? If wild cereal grasses can be harvested in unlimited quantities, why should anyone bother to till the soil and plant the seed?

5. Concepts of domestication

If there had been a clear-cut and dated start to domestication then this date could be matched with, for examples, palaeoclimates. However, it is widely recognized that there is no such clear-cut event. For cereals, the change from wild to domesticated cereals did not take place rapidly: domestication was a protracted process, rather than an event. No single answer about time of domestication is possible. Separate information from barley and einkorn indicate a protracted transition of up

to 3000 years [59]. A more detailed review argued that the different characters thought to be diagnostic of domestication evolved at different rates [60]. For example, grain size and shape evolved 1000–2000 years prior to non-shattering spikes. A further qualification and an additional layer of complexity was recently added by the suggestion of multiple domestications, with varying strengths of selection at different points of time and across distinct geographical regions, with a number of different processes in action [61]. A detailed analysis of selection coefficients for emmer concluded that it was possible to estimate the origins of selection—that is, the incidence of non-shattering—occurring between 18 346 and 25 606 BCE. For barley the figures were between 10 405 and 10 705 BCE in the Northern Levant but older in the Southern Levant at between 17 881 and 21 792 BCE. As domestication proceeded an evident change in the strength of selection in Near Eastern cereals was found around 8000 BCE, but this did not apply to the Southern Levant, where there was no increase in selection strength over time.

These remarkable results indicate that the selective processes driving crops down the domestication-evolution trajectory extended back in time beyond our currently accepted dates for the first appearance of domesticated phenotypes. In essence, it is impossible to say when domestication took place. These results do not conflict with the suggestions in this review (above) that LAM-syndrome wild species provided a model for the first cultivation of cereals (and that the syndrome itself was natural and long-standing).

6. Human management of LAM-syndrome wild cereals: before the first fields

As LAM-syndrome grasses were probably adapted to regular natural fires, the influence of anthropogenic fire in the course of human management of wild cereals would be difficult to prove or disprove. Even if it could be shown, the purpose of vegetation burning by humans could have been providing pasture for wild game or clearing dense woodland, an activity going back perhaps 100 000 years [62].

Although there is no certain evidence, it is probable that human harvesting of LAM grassland had some impact. For example, the use of sickles allowed the removal of entire heads of seed and would increase the proportion of shattering plants in the population (from seeds that escaped the harvested seed head), whereas beating seed into a container would remove shattering seed and increase the incidence of non-shattering plants in the population. There is a possible sign of this harvesting effect at Ohalo II, the 19 400-year-old site on the shores of the Sea of Galilee, where 36% of wild barley and 25% wild wheat rachises were found to show non-shattering.

Other possible human impacts on LAM grassland may be impossible either to quantify or to distinguish from natural events. Overharvesting by humans would obviously reduce the ability of the harvested annual species to survive, as would the lack of human control over grazing of young LAM-syndrome species by wild ungulates. There is potential for a major impact on the ecology of wild cereals through controlled grassland burning after harvest but no direct evidence. But in any case, human burning would be a mimic of natural fires and would not induce evolutionary changes in the wild cereals.

Originally local seed movement by humans could have been accidental, either by taking harvested material to the home base for de-chaffing and husking (needed for early cereals) and then throwing away seed accidentally with discarded chaff; or by using chaff as a temper for unfired mud-brick buildings [63], where remnant seed could germinate when buildings became derelict. Translocation could even be long-distance, as extensive trade in gathered grain from wild grasses continues to this day in Africa [64].

Human dispersal of crops beyond the area of their wild relatives allowed the subsequent divergent evolution of the crop. Spatial separation restricted gene flow between the old and the new location, thereby preventing genetic swamping by gene flow, allowing adaptive radiation, and eventually allopatric speciation [65]. However, the greatest source of variation would have resulted from the pronounced ability of traditional farmers in recognizing and propagating genetic variants in the crop, and their ability to keep a variety pure by 'the most finicky selection of seed ears and the pulling out of plants which are off type' [66, p. 186]. Wild-type characters redundant under human management, notably awns formerly used to bury seed, would be lost over time. An additional evolutionary bonus of an isolated population is that it is under reduced pressure from coevolved pests and diseases encountered by the original population (this ability to escape from biotic pressures is the reason for the main areas of production of major economic crops being usually far removed from the regions in which they originated [67,68]).

7. Field management by a mimic of the natural niche

Even within the ecologically robust grass family [38], LAM-syndrome grasses are distinctive as having the disturbance-related features of unusually large seeds, awns, a natural capacity for monodominance, and an annual habit, as, of course, do our first cereals. This review claims that the first fields were a managed *mimic* of an entirely *natural niche* (MNN), the naturally disturbed ground occupied by monodominant wild cereals.

This MNN view is supported by the incidence of non-shattering (domestic type) over time. Northern populations of barley in the Fertile Crescent stayed shattering until later than 8000 cal BCE then within 1000 years became non-shattering (domesticated type). Similarly, einkorn populations were 100% shattering at 8500 cal BCE but 100% non-shattering by 6500 cal BCE [61] (electronic supplementary material, figures S2 and S6). That is, judged by incidence of non-shattering (a supposed indicator of domestication), plants with wild-type characters were a source of human food several thousand years after the time of their presumed domestication.

There were two requirements for human field management to approach a close mimic of the environmental conditions governing the growth of wild cereals. First, there was the need for an annual disturbance of the habitat ploughing and tilling and even burning to destroy perennial weeds and weed seed [69]. Such post-harvest field burning continues to the present, for example in the chitemene shifting cultivation in Zambia [70]. Second, and obviously, as cereals became non-shattering, physical separation of seed and then sowing was needed to protect cereal seed by burying (and further control small-seeded weeds that could not emerge from deep burying).

8. Validation of present-day cereal farming

There is extensive evidence—partly reviewed in our section above on 'monodominant grassland'—that wild grasses are capable of becoming ecologically dominant to the extent of excluding other species. The suggestion was made by May that there was no reason to expect simple natural monodominance to be unstable but added a warning that crop monocultures may lack the evolutionary pedigree of natural monodominance, a reasonable warning at the time [71]. May's concern over the lack of an evolutionary pedigree is fortunately unfounded: the LAM syndrome, which our earliest domesticated cereals embodied, has an evolutionary pedigree of monodominance going back probably to the Miocene and certainly pre-dates the time of the first cultivation of cereals.

9. Other cereals with a LAM pedigree

Apart from the three LAM-syndrome founder cereals (einkorn, emmer and barley, all from the grass tribe Triticeae) there are other cereals that may have followed a similar pathway to domestication. These include oats (*Avena sativa* tribe Poeae), rye (*Secale cereale* tribe Triticeae) and rice (*Oryza sativa* tribe Oryzeae). Three wild relatives of these are awned, with awns capable of seed-burying: *Avena sterilis* (seed weight 50.2 mg) with geniculate, twisted, awns; *Secale montanum* (seed weight 12.1 mg); and *Oryza rufipogon* (seed weight 13.2 mg) with scabrous awns (as in einkorn, emmer and barley) [28]. All three wild relatives have long, relatively narrow seeds, an adaptation for seed burying; all three can form monodominant grassland.

Maize (*Zea mays* subspecies *mays*) evolved from *Zea mays* subspecies *parviglumis* (teosinte). Teosinte is not a LAM-syndrome grass: its pathway to domestication would have been different. There are no awns to bury seed: seed protection is by means of a camouflaged and 'stony' seed coat, reducing the chance of being eaten by seed-eaters and also of being damaged by fire.

10. Explanatory power of the LAM syndrome versus niche construction theory

The emerging concept of niche construction theory (NCT) adds complexity to the origin of cereal agriculture. It was suggested that NCT provides a powerful conceptual framework for understanding how and why humans and target species entered into domesticatory relationships [72–76]. However, these are the views of anthropologists, that is, an anthropocentric concept of NCT—with humans providing an ecological niche for the first cereals. This limited view suffers from three fundamental problems.

The *first problem* relates to a general definition of NCT, where two criteria were suggested [77,78]:

— Humans must significantly modify environmental conditions.
— Human-mediated environmental modifications must influence selection pressures on a recipient of niche construction (in our case, the wild relatives of our first cereals).

However, this present review strongly suggests that the management of the first fields was—indeed, had to be to succeed—a close mimic of the natural ecology of wild cereals.

Therefore, the environmental conditions were not significantly modified by humans, rather the opposite. The first criterion has not been met.

In the absence of significant environmental modification by humans there would have been no change in the environmental selection pressure on the wild cereal grown in the first fields and no evolutionary consequence. The second criterion has also not been met. As neither criterion has been met NCT cannot be applied to the first cereals in the first fields.

The *second problem* with NCT is that proponents claim that a great range of species were repeatedly 'auditioned' in a wide range of different potential forms of intervention to identify new and better ways of shaping and enhancing their niche [79]. This is describing supposed human behaviour more than 10 000 years ago: no evidence is ever presented. A more parsimonious interpretation, based on the ecology and adaptive nature of LAM-syndrome wild cereals (an obvious source of food), was that very few wild cereals—initially three species—were brought into cultivation under field management which was a very close mimic of their natural ecology. No great range of species, multiple auditioning, or different forms of niche construction was needed.

A *third problem* with NCT would be to identify when in the archaeological record humans began to modify ecosystems in a substantial and sustained manner [77]. There is an admission by a proponent of NCT that human niche construction involving non-domesticated or wild species often mimics natural events and processes, making it difficult to differentiate between the two. For example, many of the specific methods of human niche construction represent anthropogenic analogues to events, processes and landforms that occur in nature—fire clearance of trees and grasslands, forest clearings owing to windfalls, flood-scoured sand banks [75]. At least initially, these entirely natural disturbed conditions could have been used by humans for growing the first cereals by a process of niche *selection*, rather than niche *construction*. Specifically, direct evidence of fire management for the purpose of field management is needed to support claims of NCT [80].

This review of LAM-syndrome grasses and their role in the origin of the first cereals therefore contests the claim, as recently pursued by anthropologists, that NCT can offer a 'powerful conceptual framework' to understand the origins of cereal agriculture [76,81]. Significantly, the anthropological view admits that NCT encompasses the niche-altering activities of all organisms, but then sees humans as the ultimate niche constructors [82]. A more nuanced claim, by an evolutionary biologist, is that the core idea of NCT is of the evolved properties of organisms making some aspects of the environment relevant sources of natural selection, and screening off others, thereby helping to shape and constrain likely paths of the population's evolution [65]. In this view no mention is made of humans.

Instead of a questionable focus on human behaviour and NCT, a plant-centric explanation of domestication is possible, based on the LAM syndrome and the natural ecology of wild cereals. That is, rather than humans being the ultimate niche constructors, as claimed [82], the wild cereals determined their own niche requirements: they grew in, and were adapted to, natural niches maintained by natural disturbance in a limited region defined by the natural distribution of each wild cereal species. As explained above, a key requirement for humans cultivating the earliest cereals was to make the cultivated niche resemble, as closely as possible, the long-standing natural niche in its pattern of disturbance, disturbance that of necessity continues to this day in arable farming. The ecological requirements of wild cereals determined the form of this niche, not humans.

What followed, when humans dispersed cereals away from the natural distribution of their wild relatives, was a mutualistic relationship between crops and humans. Crops gained a far larger area of production compared to their wild relatives; human management by a mimic of the natural niche allowed ownership of a greater and more reliable food source.

11. Conclusion

This review describes a rare natural syndrome shown by three wild grass species ancestral to the first three domesticated cereals: all three have large seed and seed-burying long awns, and are capable of monodominance (LAM syndrome). It is suggested: (i) that fire or physically disturbed soils provided the selection pressure for the spread of LAM-syndrome annual grasses; that environmental disturbances at the time of the Pleistocene to Holocene transition and later [82] allowed the spread of such grasses [83]; (ii) that the form of natural disturbance conditions under which such grasses thrived was closely copied by farmers of the first fields in a close mimic of the natural niche; and (iii) that as the Holocene climate allowed the spread of trees, there was the increasing need to obtain grain from managed fields (as opposed to wild cereals, which were being displaced by trees). Human management of wild species in fields allowed the selection of favoured characters (plumper seed) and the loss of now-redundant features under relaxed selection [84] (notably shattering and awns—the loss of the latter still not complete). It could be argued that the seed-burying awn is the single most important feature of the grass family (Poaceae) in relation to cereal domestication and the initiation of global agriculture.

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