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RESEARCH ARTICLE

Open for Competition: Domesticates, Parasitic Domesticoids and the Agricultural Niche

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This paper explores the relationship of weeds and crop parasites in the domestication of crop-plants within the Old World, drawing predominately on China and the Near East. This relationship is explored using the concept of niche construction in which the act of cultivation sets about chains of feedback in which the ecological worlds of plants and humans became increasingly intertwined resulting in ever increasing spheres of interdependence. Into this domestication entanglement a number of peripheral organisms (termed parasitic domesticoids) were drawn, from the weeds which came to inhabit arable fields, to the insect pests and rodents that came to settle in the grain stores of the first farmers. The evolution and spread of these organisms is then outlined against that of the crop itself.

Introduction

There is no doubt that the suite of human activities involved in cultivation created environments that would not otherwise exist, and non-human organisms have adapted to these environments. The adapted, co-evolved organisms include domesticated plants (true domesticates) as well as what we will refer to as domesticoids, comprising taxa that tagged along becoming also increasingly part of the cultivated environment. These domesticoids include weeds and crop pests. In terms of biological coevolution, domestication creates a symbiotic relationship, in which both organisms, crops and people benefit in terms of reproduction

and population increase, whereas domesticoids are parasitic in that they prosper at the expense of domesticates and humans. These categories are not necessarily fixed for all time, as crops can become weeds and vice-versa some weeds have become crops. These categories can be applied beyond the plants in the field, in that other organisms, such as rodents and insects can be considered in these terms. While terms such as synanthrope or commensal are often applied to such taxa, we suggest that parasitic domesticoid is more fitting, as these taxa have undergone adaptions that parallel domestication, making them increasingly dependent on the human created niche of agriculture and sedentism, and parasitic in that they derive their nutrients at the expense of the cultural food production. In other words the culturally maintained and transmitted agricultural niche

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is integral to their survival, and they are more than mere fellow travellers.

Niche Construction has become widely accepted as a useful conceptual framework for the discussion of plant and animal domestication (e.g. Fuller and Lucas 2017; Scott 2017; Watkins 2017; Zeder 2016). Cultural niche construction implicates processes of change via feedback between culturally transmitted practices, long-term modifications to the environment (clearance, arable soils, etc.), and genetic evolution in various organisms, not just the human associated taxa that were the targets of domestication, but fellow travellers, opportunists, and even unseen micro-organisms.

The present paper explores the entanglements between the evolution of cultivation and storage practices with the adaptations in crops, weeds and pests. First, how the domestication syndrome of traits in seed crops adapted them to cultivation and provided increasing returns to yield, but in doing so forced increased human effort which manifested in the evolution of cultural practices and technologies. Second, how the arable ecosystem constructed new communities of parasitic domesticoids, a category applied to storage pests and weeds, with some of the latter eventually converging on and becoming true domesticates. Taken together these entail that arable systems, and the social systems that maintained them, acquired an increasing number of innovations that were transmitted through a combination of genetics, environment and culture.

Transformation to the Agricultural Niche: Hook and Pull

Domestication transforms crops and species so that they are better adapted to being planted and harvested by people, and a set of recurrent parallel adaptations is found across species. In grain crops, planted from seed and harvested for their seeds, there is a well-documented domestication syndrome: including loss of automatic seed dispersal, loss of germination inhibition or seed dormancy, increase in seed size and reduction of seed dispersal aids likes barbs and awns (Harlan, de Wet and Price 1973). While these changes 'improve' crop plants, they come with costs, in that they entrap people in new forms of labour, including maintenance of soil fertility and new steps in crop-processing (Fuller, Allaby and Stevens 2010; Fuller and Lucas 2017; Fuller et al. 2016). Growth in archaeobotanical evidence and refinements in methods have made it possible to document not just the presence but also the quantitative increase in these traits over time, allowing rates of change to be estimated (Fuller et al. 2014). Such information in turn can then be related to archaeological context and innovations in technology, techniques and labour organization of subsistence.

Cultivation comes in a wide range of forms but clearance of pre-existing vegetation and disturbance of the soil is largely universal. More intensive forms of cultivation can be expected to remove all pre-existing visible vegetation and, through digging and turning the soil, influence below ground biomass in terms of tubers and the seedbank. The axe, simple digging sticks, and fire, together with human effort, can achieve this (Steensberg 1986). Cultivation creates a habitat in which annual disturbance is both uniform and highly predictable, sunlight penetrates to the soil, becoming available for growth and germination, and evapotranspiration often increases. This creates a scenario of altered-competition, in which plants adapted to rapid germination are favoured and faster growing plants from more rigorous seedlings can quickly shade out their neighbours, perhaps related to increased seed size (Harlan, de Wet and Price 1973). Tillage also creates deeper cracks which may bury seeds more deeply than they would be if they had fallen on natural soil surfaces, for which larger seeds with more nutrient reserves may also have an advantage.

Comparisons across taxa, including those cultivated as vegetables or tubers, indicates that increased seed size is a recurrent trait of domesticated species (Kluyver et al. 2017).
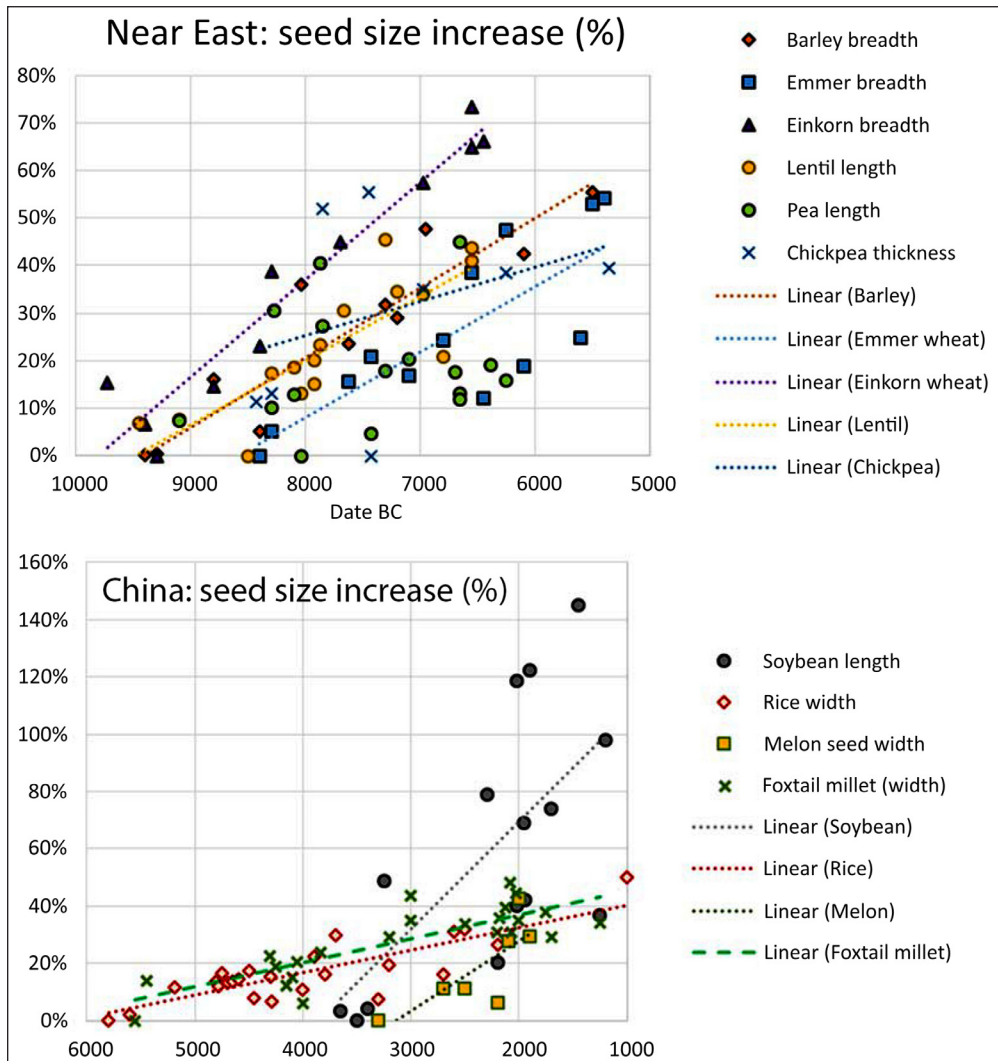
Figure 1: Showing size increase plotted on the Y-axis against time on the X-axis for the major crops from the Near East (top) and China (bottom). Average grain and seed size data for given sites and time periods from archaeobotancial data based on that in Fuller et al. 2014.

Archaeobotanical data for several species clearly documents this increase in average seed size over the millennia of early cultivation (**Fig. 1**). While increased seed size may sometimes be linked to genetic changes favouring other organ enlargements, it appears rather as a selected trait, part of a general strategy of nutrient acquisition, including higher growth rate, highly adapted to the nutrient-rich, bare soils and open habitats of competition found in early cultivated fields. Thus

cultivation by providing a predictable resource base for plants promotes a shift to nutrient-acquisition strategies that can be contrasted with nutrient conservation strategies seen in more stable environments (Milla et al. 2015).

In turn increased seed size pulls farmers into a greater commitment to cultivars. Larger seeds have a higher caloric value, augmented by an increased number of grains per ear or panicle harvested. However,

to support this increased yield, each plant requires more resources: soil nutrients and water, hence human efforts towards supplying these must also increase. Some of the earliest farming ecologies took advantage of soils naturally replenished by annual flooding. These include many early Pre-Pottery Neolithic sites in the Levant, inferred from site locations (Scott 2017: 66; Sherratt 2007), and the *decrue* rice agricultural systems of China in use prior to evolution of domesticated, non-shattering rice (Fuller, Weisskopf and Castillo 2016; Weisskopf et al. 2015). But as cultivation expanded, and crops became morphologically closer to domesticated forms, thus more demanding, intensive management of soil conditions became necessary, as inferred for rice based on early field systems and associated phytolith indicators (Fuller and Qin 2009; Weisskopf et al. 2015), and for early Near Eastern/European wheat and barley based nitrogen isotopes from archaeological grains (Bogaard et al. 2013; Styring et al. 2017).

Parasitic Domesticoids: Weeds and Storage Pests

Cultivation also created ecological niches for taxa that were not consciously favoured by people, so-called weeds and pests that became feared and despised. Over the long term these have been major players in human history, unintentionally transported through human agency, and creating landscapes of invasive ecological communities. We can refer to these taxa as *Parasitic Domesticoids*, as they share many adaptive features with domesticates, while they are parasitic in that their success comes at a cost to humans; weeds competing with growing crops, animal and insect pests obtaining their calories from human stores.

Weeds are a key beneficiary of the arable niche. While a 'weed' is only generally defined in relation to human perspective as a plant growing where it is not wanted, there are recurrent adaptations shared across these species (Bunting 1960). Just as increased seed size and rapid germination are aspects of nutrient acquisition strategy favoured by

crops in cultivated fields, weeds have similarly been selected for such environments. In particular this has favoured the spread of taxa with transient seedbanks, which either germinate shortly after sowing, characteristic of larger grained grasses and forbs of seasonally dry grassland (Type I), or after winter, often characteristic of seasonally disturbed coastal and mountain habitats (Type II) (Thompson and Grime 1979). In contrast are those weeds with persistent seedbanks (Thompson and Grime 1979) in which a large dormant population is maintained in the soil (Type IV).

These two contrasting ecologies, along with intermediate seedbank form (Type III), are important in shaping the early agricultural weed floras (**Fig. 2**). Type I characterizes such common weeds as wild oats (*Avena* spp., although some species possibly developed intermediate strategies) and other grasses (*Bromus* spp, *Lolium* spp., *Phalaris* spp.), knapweeds (*Centaurea* spp.), cleavers (*Galium aparine* and *tricornatum*) and corncockle (*Agrostemma githago*), while Type IV includes taxa such as small legumes (various *Trifoliae*, *Onobrynchis*), knotweeds (*Polygonum* and *Rumex*), poppies (*Papaver* spp.), and fumitories (*Fumaria* spp.). Those with Type I or II seedbanks often have larger seeds, more likely to contaminate grain stores and be sown with seedcorn, while Type IV remains competitive through their persistent seed banks (**Fig. 2**). Several of the aforementioned taxa are now known to have been harvested alongside the earliest crops, even before the morphological changes of domestication are present in crops (Willcox 2012), and became well established alongside domesticated cereals during the later Pre-Pottery Neolithic (Harttman-Shenkman et al. 2015). Many species in these genera (and others) came to exist largely under anthropogenic cultivation, what Zohary (1950) referred as obligate weed flora, or 'homeless' species, in the sense of no longer having a wild, non-anthropogenic habitat. These weed species are now hitchhikers of cropping cycles, dependent on
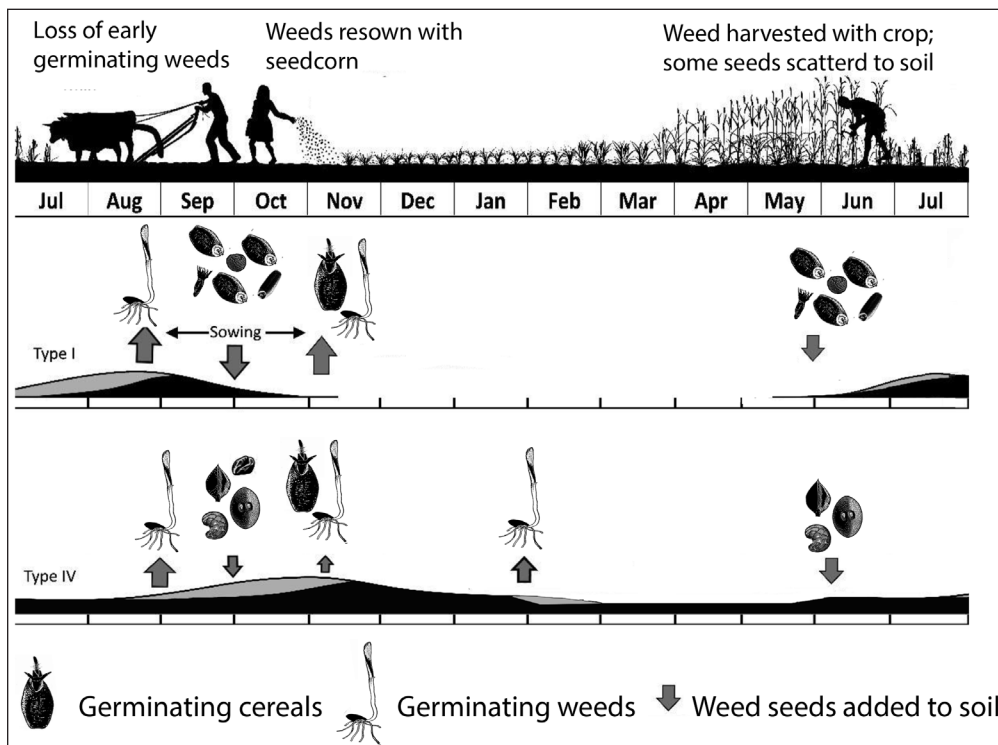
Figure 2: The relationship between the two major seed banks (Type I and Type IV) with the autumn sown crop cycles. Indicating periods of germination (losses from the seed bank) mainly relating to tillage, and additions to the seedbank from sowing and seed setting prior to and during harvest.

the anthropogenic maintenance of arable environments.

These taxa also presumably underwent evolution towards emphasis on arable weed (domesticoid) traits during the origins of agriculture, just as crops became domesticated. This is most evident in taxa that apparently did not exist prior to agriculture, or which evolve new varieties especially adapted to agriculture. For example, *Lolium temulentum*, which has longer grains than most congeneric grasses and thus mimics barley grains, first occurs in the Levant towards the end of the Pre-Pottery Neolithic, with examples from Atlit Yam (ca. 6900 BC) and Ras Shamra VC (ca. 7100 BC) (Hartmann-Shenkman et al. 2015; van Zeist and Bakker-Heeres 1986). Although it is predominately self-pollinating, like wheat and barley, it is interfertile with *L. remotum*, an obligate flax weed across

Northern Eurasia, and *L. persicum*, which has a broadly Middle Eastern distribution from Baluchistan to Anatolia. Some earlier *Lolium* finds had shorter grains, like *remotum* or *persicum*. Thus it seems likely that *L. persicum* invaded early cultivated fields, differentiating into *L. remotum* in flax and *L. temulentum* in cereal fields. Similar stories can be reconstructed for some of the wild oats (e.g. *Avena fatua, Avena vavilovii*) or rice mimicking forms of barnyard grass (*Echinochloa oryzicola*) or flax mimicking *Camellina sativa* var. *linicola* (Barrett 1983), all of which are rare outside of cultivated environments. In some cases these weeds were so successful that farmers adopted them as crops, creating domesticated forms, such as cultivated oats (*Avena sativa, A. abyssinica*) (Loskutov 2008), or the rare domesticated *Echinochloa macrocarpa* (de Wet et al. 1983).

Entering the Storage Niche

Another key component of agricultural systems is grain storage, which created a fundamental habitat for many other parasitic domesticoids including small mammals and insects. The house mouse (*Mus musculus* subsp. *domesticus*) appears in animal bone assemblages in the Levant by the Early Natufian period (15,000 BP), where it is favoured in long-term, sedentary occupations over other forms of mice (Weissbrod et al. 2017). House mouse rose from less than 5% before 9500 BC to >80% of all identified small mammals in the Levant by the Middle Pre-pottery Neolithic B (PPNB) (ca. 8200–7500 BC) (Cucchi, Auffray and Vigne 2012). This rapid rise in commensal mice correlates with both increasing reliance on cereals across many sites (Maeda et al. 2016), the appearance of increasingly larger sites (**Fig. 3**), and more readily recognizable evidence for storage bins within houses (Kuijt 2011). Prior to this a few sites have apparent communal storage buildings, such as at Jerf el Ahmar, where alongside evidence for arable weed flora and crop-processing, droppings of house mouse increase at the expense of other rodent types (Willcox and Strodeur 2012). As demonstrated by comparing assemblages from relatively mobile Late Natufian and pre-Natufian sites with those of the increasingly settled Early Natufian and Neolithic, the *domesticus* house mouse tends to exclude other taxa in the more settled contexts, but declines or disappears on sites where humans are more mobile (Weissbrod et al. 2017). This implies that there were traits inherent in this species, which rapidly evolved prior to cereal domestication and gave it an edge over other rodents, but also obligated this mouse to its human association. In East Asia too, *Mus musculus* subsp. *castaneus*, of India, Southeast Asia and South China diversified and spread after a bottleneck estimated at 7600 years ago, based on modern genetics (Suzuki et al. 2015). The similarity in date to the early stages of rice domestication is suggestive (Fuller, Weisskopf and Castillo 2016), although details of geographical dispersal remain to be worked out.

Once such pests were established in human settlements, this in turn provided an attractive habit for a predator of such pests, namely the cat (*Felis domesticus*). The wild cat was a denizen of woodlands, rich in birds and small mammals, but invaded the new niche of human villages, which had come to attract mice, other rodents, as well as sparrows, pigeons, etc. Currently the earliest evidence for cats comes from the start of the PPNB (ca. 8600 BC) on the Island of Cyprus (**Fig. 2**), where house mouse and cat both appear to have been introduced, along with morphologically wild wheat and barley, with human colonists from the mainland (Vigne et al. 2012). While evidence for cat is not yet reported on mainland Near Eastern sites, we must infer that this small carnivore had already moved into the village niche prior to its translocation to Cyprus. While we are safe to assume that mice were recurrent stowaways on boats to Cyprus (Cucchi, Auffray and Vigne 2012), the cat presumably was an intentional component of the humans' portmanteau. Interestingly, the house mouse does not appear to have made it to Neolithic Greece, implying perhaps that some developments in settlement pattern, storage or cleaning boats may have kept the mice at bay, although they were spread throughout the Mediterranean during the Bronze and Iron Ages.

Another major source of storage pest is found among the insects. A wide range of beetles, moths and other insects readily infect stores of grains or pulses (Gorham 1987; Kislev 1991). A group that illustrates a process of adaptive evolution into the new niche afforded by grain stores are the grain weevils (*Sitophilus* spp.), including the so-called corn weevil (*S. zeamais*), rice weevil (*S. oryzae*) and the granary weevil (*S. granarius*). These closely related species have followed pathways of parallel evolution, and are found mainly or entirely in grain stores today. Their Latin names reflect where they were first encountered by taxonomists rather than any inherent food preference. The tamarind weevil (*S. linearis*) is another
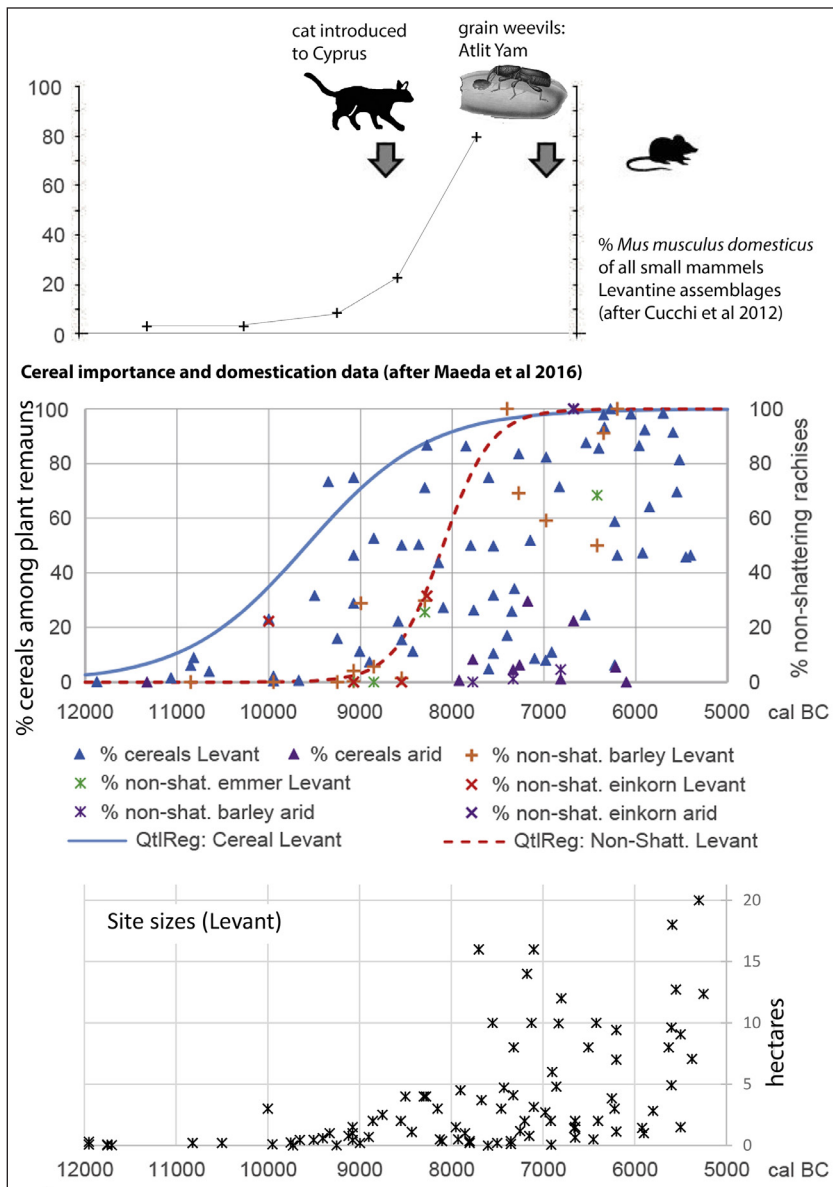
Figure 3: Relationship of animal parasitic domesticoids (% of *Mus musculus*) and earliest grain weevils (top from Cucchi et al. 2012) with shattering data (% of non-shattering domesticated rachis types), and % of cereal remains to all other charred remains (middle from Maeda et al. 2016) and site size (in hectares) for the Near East (bottom from authors' own data).

related pest of some tropical fruits and seeds, while the rest of the genus consists of 10 species, largely confined to Eurasia and infecting mainly the acorns of oak trees, or a limited range of trees, for example tropical Asian Dipterocarps and tree legumes (Plarre

2010). From an ancestral preference for nuts and tree fruits, three of these species have moved into the human-constructed agricultural niche.

The primary dispersal mechanism for these three grain store species is human transport

of grain, either moving infected grains to new stores or adding fresh grain to infected stores. These snout-nosed beetles chew cavities into seeds, deposit and seal-in their eggs, from which the larvae emerge and feed on the interior of the grains. In most cases the adult form is dispersed by flight, but *S. granarius* is entirely flightless and *S. oryzae* is largely so (Plarre 2010). Panagiotakopulu and Buckland (2017) hypothesize that *S. granarius* might have originally been adapted to rodent nests, adapting with rodents to stores of grain, however, it seems likely that loss of flight represents evolution through the long association with human storage. *S. oryzae* likely evolved in parallel, but has had some millennia less, as rice domestication is younger than wheat and barley (Fuller et al. 2014). In Asia *Sitophilus* grain pests probably first invaded the agricultural storage niche with tree nuts, perhaps the acorn stores of hunter-gatherers who initiated early cultivation. All three aforementioned weevils also share a preadaptation to this anthropogenic niche in the form of symbiotic bacteria that help them to digest carbohydrates under conditions of very little moisture (Plarre 2010), as characterises cereal stores, which potentially explains why other weevils in this genus never made this transition to storage pests.

Archaeological evidence is patchy but indicates both the association of *Sitophilus* with nut-storing humans, notably in Japan, and the long association in the Near East of weevils and grain stores. Alongside impressions of seeds in Jomon ceramics, maize weevil impressions have been recovered among the earliest Jomon, ca. 8500 BC, a period in which plant subsistence was largely nut based, including acorns (Obata et al. 2011). Much larger quantities have been found from Western Japan at the end of the Late Jomon (*c.* 1500–1000 BC), the period in which contact with the Asian mainland had begun and by the end of which Chinese rice and millet crops were potentially introduced. Subsequently these maize weevils must have moved into grain stores and spread to mainland Eurasia.

By contrast, the semi-flightless rice weevil can be suggested to have moved from acorns to rice in the Chinese rice domestication region (Yangtze basin), where rice was cultivated for millennia alongside acorn gathering, with a shift to reliance on domesticated rice ca. 6000 years ago (Fuller and Qin 2010; Fuller, Weisskopf and Castillo 2016). At present the only published rice weevil find is from a Han tomb (2nd c. BC) (Obata et al. 2011; Panagiotakopulu and Buckland 2017), but the potential to develop systematic sampling for insect remains from Yangtze sites, where waterlogging is sometimes present, is high.

Evidence for grain weevils in the Near East and parts of Europe is much more extensive (Panagiotakopulu and Buckland 2017). The earliest evidence is from later Pre-Pottery Israel, ca. 6900 BC (**Fig. 2**), alongside stored crops and many obligate weeds at Atlit-Yam (Hartmann-Shenkman et al. 2015; Kislev, Hartmann and Galili 2004). Subsequent Neolithic finds in Turkey and Greece suggest association with the spread of crops, which reached as far as central Europe during the Early Neolithic (Panagiotakopulu and Buckland 2017). As with grain storage, these pests require warm and dry conditions to persist, implying indoor, above ground storage in Early Neolithic longhouses, whereas grain weevils are absent from further north and west in Europe, introduced apparently only in the Roman period, a period which saw extensive shifts away from prehistoric pit storage. This highlights the role of storage practices, whether intentionally or inadvertently, in constructing or obstructing the ecology of these pests.

Concluding Remarks: the Agricultural Niche as Battlefield

The examples explored above highlight how practices associated with Neolithic subsistence transformations opened up a niche for plants and animals to evolve into. The arable field is an open field, which invited seed competition within crops, leading to increased grain size, and fostered competition from

a range of uninvited herbaceous species (weeds). This required increased human labour inputs and the competition between crops and weeds became an unending 'botanical battlefield' in which innovation in cultivation practice (e.g. tillage systems) can be seen as a coevolutionary arms race between farmers and weeds (Jones 1988). Similarly, storage necessitated by cultivation also opened a new field of battle between commensals, mice, weevils and others—with humans for the calories contained in those stores. The taxa that invaded this niche were parasitic on human economies and evolved many traits that paralleled those of the domesticated taxa of food production; thus *parasitic domesticoid* is a more apt term than synanthrope or commensal. The domestication of cats, the evolution of rodent catching dog breeds, and changes in storage techniques can also be conceived in terms of a coevolutionary arms race within the environment of sedentism and food storage. Thus domestication was only one of the outcomes of the niche construction activities that started in the Neolithic, as these new niches created obligate parasitic domesticoids, and an ongoing challenge to cultural innovation to minimize the economic 'damage' domesticoids bring. Humans transported and reproduced these battlefields of the arable and sedentary environments through Neolithic dispersal, often fostering new climatic adaptations for the involved taxa in the process (Fuller and Lucas 2017).

Certain parallels are striking. Weevils and weeds with transient seedbanks evolved to rely on humans as a means of dispersal, thus parallel to the evolution of non-shattering in domesticated cereal crops. Weevils, mice and cats can all be regarded as having shifted from a wild preference for oak woodlands, as can several weeds originating in woodland margin habitats, into the novel open spaces of arable fields and enclosed spaces of villages. As agricultural economies could support denser populations, encouraging population growth, the size and number of agricultural villages grew, thus transmitting the cultural constructed niches of field and settlement. Over the long-term woodland was reduced to make way for farming and thus these few species who had transferred their habitat allegiance to the agricultural milieu from their ancestral woodland homes did very well, and they were able to spread geographically beyond their origin ranges as farming cultures and their crops expanded. This translocated agricultural environment was one of recurrent soil disturbance and high nutrient availability, both in the tilled soils and the settlement stores, and as such it diverged from the expectation of stable environmental conditions and more conservative use of nutrients that is more typical of long-established ecologies, like climax woodlands. Parasitic domesticoids, crops and humans all dwelled in an environment that was tilted towards resource acquisition strategies, underpinned by human labour costs, and rife with competition – from the calm and stable woods to the hustling village.

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Competing Interests

The authors have no competing interests to declare.

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