REVIEW

Plant domestication and agricultural ecologies

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Plant life defines the environments to which animals adapt and provides the basis of food webs. This was equally true for hunter-gatherer economies of ancestral humans, yet through the domestication of plants and the creation of agricultural ecologies based around them, human societies transformed vegetation and transported plant taxa into new geographical regions. These human–plant interactions ultimately co-evolved, increasing human population densities, technologies of farming, and the diversification of landraces and crop complexes. Research in archaeology on preserved plant remains (archaeobotany) and on the genomes of crops, including ancient genomes, has transformed our scientific understanding of the complex relationships between humans and plants that are entailed by domestication. Key realizations of recent research include the recognition that: the co-evolution of domesticates and cultures was protracted, the adaptations of plant populations were unintended results of human economies rather than intentional breeding, domestication took place in dozens of world regions involving different crops and cultures, and convergent evolution can be recognized among cropping types — such as among seed crops, tuber crops, and fruit trees. Seven general domestication pathways can be defined for plants. Lessons for the present-day include: the importance of diversity in the past; genetic diversity within species has the potential to erode over time, but also to be rescued through processes of integration; similarly, diversification within agricultural ecosystems has undergone processes of decline, including marginalised, lost and 'forgotten' crops, as well as processes of renewal resulting from trade and human mobility that brought varied crops and varieties together.

Introduction

The emergence of agriculture was transformative of our species' relationship to our planet[1,2,3]. We created new ecological niches of agricultural systems that became hotspots of coevolution (as defined by Thompson[4]), in which domesticated plants and animals evolved together with a range of commensals, also referred to as parasitic domesticoids[5] — namely, species such as animal pests (mice, house sparrows, grain weevils, etc.) and arable weeds that draw their calories out of the crop–human system. These new agricultural ecologies can be thought of as transformations of food webs[6,7], whereby more energy from the primary productivity of the ecosystem, ultimately derived from photosynthesis, was channelled into growing populations of domesticates, domesticoids and humans. In turn, these agricultural ecologies often supported increasingly sedentary human populations at increased population densities, increased populations of domesticates and expanded geographical ranges of domesticated crops, as well as the domesticoids. While domestication as a form of food production through the coevolution of mutualistic relationships is not something new — such coevolutionary relationships have evolved may times over the past 50 million years, among ants and fungi, termites and fungi, various wood boring beetles and fungi, ants and aphids[8,9] — but whereas insect–fungus agriculture tends to involve a co-evolved pair of species, the long-

term history of human agriculture and the domestication processes connected to it involved many species entangled interdependently and a growing diversity of species over time.

Human agriculture transformed not only regional landscapes, but also the earth system, such as the increases in greenhouses gases that are detectable since the middle Holocene, 8000–4000 years ago[10]. This middle Holocene period saw widespread expansion of the geographical range or crops, and many local transitions to cultivation. By 2000 years ago, agricultural transformations were extensive on several continents[11]. In several regions, the nature of human land-use 2000 years ago provides a robust context for predicting current biodiversity patterns, even though subsequently overlain by recent industrial era transformations and climatic fluctuations[12]. Agriculture potentially offers one of our greatest tools for maintaining sustainability of so-called ecosystem services and high human populations, but this may require new approaches to domestication and different agricultural ecologies than those that dominate the present world. The written history of agriculture and the ethnographic record of traditional ecological knowledge, though important, provide only a small fraction of overall agricultural heritage (of recent centuries), while the archaeology of past agriculture can provide a much deeper framing of that heritage (of many millennia). Understanding the emergence and spread of agriculture, and the varied instances in which it occurred, can offer insights into the various paths that regional human populations and environmental histories took, and what directions they might be guided in the future.

Recent advances in research on domestication and early agriculture have been archaeological, ecological and genetic. In archaeological terms, there has been a massive increase in empirical evidence through archaeological recovery, from more crops and more regions[13–16] that allows a more quantitative approach to understanding rates of evolution under domestication[17,18], a comparison of domestication traits and syndromes among animal species[19,20] and plant species[21,22], as well as a recognition of the geographical and ecological variability within and between regions where early domestication took place. Meanwhile, the genomic revolution has also revealed complexity in processes including selection, additive functional alleles[23,24], gene flow from wild populations[25,26], and genomic rescue[27], that were largely unappreciated in the last century. Experimental approaches to functional ecology help unravel some of the selection pressures on early cultivars[28]. In this review, we highlight recent progress in documenting domestication processes through archaeological evidence, nuances in processes of selection, and population genetic consequences. We explore how patterns may differ across different kinds of crops, and the growing need to consider processes at larger landscape and regional scales, as well as in terms of metapopulations.

Defining plant domestication and excavating it: cases of seed crops

Domestication and the emergence of agriculture are both evolutionary processes, and although interconnected, they are different. Cultivation is defined by human behaviours, and practices that are inherited through culture rather than genetics, by which people prepare land using various technologies (material culture), sow and reproduce plants. While cultivation describes these practices in general, the term agriculture can be taken to refer to cultivation on a larger scale that is more routine, a focus of community lifeways that is economically central, and which may or may not also involve the management of livestock[29]. Domestication refers to the status of a plant, domesticated rather than wild, marked by adaptations to human-maintained ecology, with lifecycles linked to cultural scheduling of ecosystem management — some species, such as major cereals such as wheat, maize, or rice became more dependent on

humans for seed dispersal. The adaptations of domesticated plants are represented by phenotypic and genotypic differences from wild populations. Parallelism across species results in a domestication syndrome, of which seed crops, grown from seed and for seed, is well known (Table 1)[17,30,31]; whereas domestication syndrome traits in other types of plant are less well defined[21]. Botanical evidence on archaeological sites is most often preserved charred, and this favours hard seeds and some parts of chaff, which allows for the study of some domestication traits.

One key trait in seed crop domestication is the loss of wild-type seed dispersal in exchange for reliance on human harvesting and dispersal. This is a widely recognized trait in domesticated cereals, pulses and other crops[32,33]. It is also a trait widely documented in early cereals by archaeobotanists through the excavation and analysis of preserved rachis segments of barley and wheat[17], spikelet bases of sorghum and rice[34,35], involucres of pearl millets[36], and the evolution of the maize cupule[25]. Only in the 21st century have sufficient datasets from some of these taxa become available to calculate the rates at which populations evolved non-shattering. For example, charred rachis segments of barley from early Holocene sites in Syria, Jordan, Israel and western Iran represent populations with varying proportions of wild dehiscent and indehiscent, domesticated type rachis morphology. These archaeobotanical remains chart a regional transition from ~0% domesticated type before 9000 BC and between 50% and ~100% domesticated forms after 7000 BC[13,37,38]. A smaller number of sites provide similar patterns of temporal change in the proportion of wild-type abscission in wheats (*Triticum dicoccum* and *T. monococcum*) over the same general period. There is some evidence of a slightly later process for *Triticum timopheevi* taking place between 8000 and 6000 BC in central Anatolia[39]. Spikelet bases of rice from sites in the Lower Yangtze basin similarly indicate a gradual transition to dominance of non-dehiscent morphologies that had started before 6000 BC and was finished sometime before 4000 BC[35,37]. In Africa, recent work documenting the impressions of chaff that had been mixed as organic temper into early ceramics provides glimpses of the domestication trajectories for *Sorghum bicolor* in Sudan[34] and *Pennisetum glaucum* in Mali[36].

These examples indicate that domestication processes lasted for millennia, perhaps 3000 or more plant generations, and up to 150 human generations (Figure 1). This is substantially slower than scholars assumed at the end of 20th century, when domestication models focused on single recessive traits and inferred domestication in less than 200 years and perhaps even 20 years[41,42]. Our new understanding of the rates of domestication for several cereals is significant because it shows that the period of co-evolution subsumed swings in climate change and substantial cultural and technological changes, which indicate that the 'origins' of domestication is not attributable to a single cause, whether a climatic event (such as the Younger Dryas dry period[43,44]) or social pressures (such as social competition or rapid population growth[45]). Rather, these cereal domestications are the outcomes of extended and dynamic coevolutionary processes, namely the long-term human–plant and human–animal domesticatory relationships (Figure 2A). The selection pressures for domestication must have been dynamic, because climatic conditions, environmental transformations and cultural practices were dynamic throughout these extended domestication periods.

Another widely studied feature of crop domestication is seed size increase. Hammer[30] suggested this was a near universal trait in seed-propagated crops, and also occurs in vegetables that are not cultivated for their seeds[46]. Thus, seed size increase during early domestication is

not human-mediated selection to make the edible portion larger, but rather reflects competition among seeds and seedlings, whereby increases in the edible portion (where seeds are eaten) arise as an incidental consequence of growth environment under cultivation. Seed size is readily documented from archaeobotanical remains[13], so we have a growing list of taxa (cereals, pulses, oilseeds) from various world regions in which domestication-related size increase has been documented, evolving over a period of millennia (Figure 1B).

A third trait that can be documented archaeologically in some taxa is loss of germination inhibition, inferred from testa thinning. Crops tend to germinate as soon as they are wet and planted, in contrast to wild forms that often germinate after certain conditions have passed, including day-length, temperature, burning, or after the seed coat is physically damaged. Explaining the evolution of this trait has been controversial. Zohary and Hopf[47] emphasized parallelism with cereal domestication in terms of seed dispersal, implying gradual evolution of reduced dormancy[48]. From the (anachronistic) viewpoint of a farmer, however, high dormancy levels would greatly reduce yields (in the year of sowing), which has led to alternative hypotheses. D'Andrea *et al.*[49], for example, posited that African cowpea could have been first cultivated as green fodder for livestock, rather than for seeds. However, such an explanation is untenable for pulse domestication in settings without livestock, such as Mesoamerica (*Phaseolus vulgaris*), the Jomon era (4000–2000 BCE) Japan (*Vigna angularis, Glycine soja*)[50], or even southwest Asia, where cultivation is generally placed a millennium before widespread herding of sheep and goats[51,52]. Spengler and Mueller[53] speculated that large wild herbivores might have concentrated plants by breaking dormancy through digestion, and humans took advantage of those stands, with subsequent cultivation. Ladzinsky[54] argued for "pulse domestication before cultivation" with the idea that rare non-dormant genotypes in wild populations were discovered and propagated (see also Abbo *et al.*[55]). The prediction of this hypothesis is that thin testa, a non-dormant morphotype, should be present from the earliest cultivated assemblages, but this has never been empirically documented in any of the discussed legume taxa. The only empirical study of testa thickness in archaeological pulses is a recent x-ray tomography study of a time series of archaeological horsegram (*Macrotyloma uniflorum*) seeds from south India which document a gradual, stepped reduction in testa thickness[56], contrary to the presence of wild non-dormant forms. If early pulse planting was about managing existing stands, dormant seeds would still contribute to these stands over multi-year periods, but genotypes or phenotypes with reduced dormancy will give a strong selective advantage by contributing more to each harvest. So far, this trait has been documented also in some *Chenopodium* pseudo-cereals of both north and south America[57,58], but is otherwise generally poorly studied archaeologically. In some cases, including *Chenopodium* spp., variation and plasticity in terms of seed coat thickness and dormancy may co-exist in individual wild plant plants, in which case selection has acted through canalization, as suggested through experimental work on the lost North American crop *Polygonum erectum*[59], but is yet to be confirmed through a sequence of archaeobotanical remains.

The sum of archaeobotanical data indicates that the early domestication of seed crops represents several instances of convergent evolution. These processes require population genetic models that are more complex than simple bottlenecks, or the rapid selection of single alleles. In these ways, domestication processes appear quite distinct from those that are observed in plant breeding, which often involve rapid selection on single key alleles and clear bottlenecks. Domestication took place within populations that were themselves key resources,

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food sources, for the people affecting them, and thus generally lower selection coefficients would mean less of the food supply was eliminated by selection in each generation. In this sense, food security would favour slow processes and weak selection, which is also indicated by the relatively large number of alleles (50–100 loci) under selection during domestication — simultaneous selection across all these alleles requires weak selection if the substitution load is not to become too onerous[60].

Forms of selection and rates of domestication

The characteristics of domesticated plants can be related to different aspects of cultivation in terms of what causes them to evolve. Botanists have long discussed domestication in terms of unconscious selection, ever since Darwin[61] introduced the term as an intermediate category between methodical selection by breeders and natural selection. Unconscious selection represented the adaptation to environments that were regularly modified by the operations of people. Darlington[62] suggested that these selection processes varied as a result of different operations, including tillage conditions, sowing conditions, harvesting conditions, and modes of propagation. Recent insights are making it possible to model some of these modes of selection in population genetic terms and to test them against the empirical archaeobotanical evidence.

Harvesting methods strongly favour non-shattering cereals over wild types, with consistent selection operating against the wild form, by the fact that harvested grains get resown by farmers[41]. As explored by Allaby et al.[63], this can be regarded as environmental selection, because it creates a clear fitness threshold (non-shattering) that provides a consistent reproductive advantage, which is dampened by things like green harvesting (before wild types have shattered) or reuse of fields that have existing crop seed banks. This is expected to create a fairly consistent coefficient of selection and a gradual sigmoidal shape to the curve that charts the increase in the frequency of the selected genotype over time.

Selection under tillage and sowing conditions can be unified within a framework of competitive selection[63,64]. Darlington saw tillage as driving seed size increase, while sowing drove loss of dormancy, but both of these traits ultimately relate to the establishment of seedlings and the ability of these seedlings to compete for resources from the soil and sunlight, and outcompete other seedlings[28,32,40,62]. The gains on one individual lead to shared losses for others, such that the disadvantage for older, wild type (small seeds) increases over time as more of population becomes better competitors. At the same time the better competitors decrease their resource gains relative to each other. Modelling this scenario indicates that this should lead to accelerating selection, and likely cycles of stasis and selection as multiple alleles come into play in terms of increasing competitiveness through grain size increase. We expect this to occur as alleles of relatively large effect reach new adaptive plateaus — such a process would account for the high heritability that has been inferred for grain size[18]. The available archaeobotanical evidence for several crops, ranging from wheats and barley, to rice, sunflower, lentil and pea, largely fit this model with multiple episodes of accelerating size increase[63].

Comparing early agricultural ecologies: pathways alternative to cereals

Most advances in archaeological documentation of agricultural origins and recent advances in genetics have focused on seed crops, especially cereals. It is clear that the beginnings of food production in some world regions were based on other kinds of crops, differing in the harvested organ and the nature of reproduction. For example, domestication syndrome traits are less well understood in vegetatively propagated crops that bear underground and reproductively viable storage organs (VSOs), such as manioc/cassava (*Manihot esculenta*), potato (*Solanum tuberosum*), sweet potato (*Ipomoea batatas*), taro (*Colocasia esculenta*) and other aroids, and yams (*Dioscorea* spp.)[21]. These crops formed the basis of transitions from hunter-gatherer to agricultural systems in several tropical and montane regions, including the Neotropics[65], Andean Highlands[66], African rainforest and Ethiopia[67,68] and New Guinea[69,70], to name a few better known centres. The syndrome of domestication traits in such crops is less well understood, either in terms of genetics or in terms of archaeological documentation. Although we can compare differences between wild and domesticated forms in commercial agriculture today, the phenotypic signatures of domestication under traditional forms of cultivation in the deep past are unclear and seem to be more variable than for other crop types, such as cereals (Table 1). Consequently, vegetatively propagated field crops can be characterised as having domestication syndrome tendencies rather than traits[21]. Some of the features of vegetatively reproduced crops appear to derive from phenotypic plasticity, in responses to the ecology of cultivation, but genetic assimilation has meant that these have also tended to become fixed through a protracted coevolutionary process. As an example, studies of manioc (*Manihot esculenta)* have found domesticated forms are less plastic in shady conditions than wild forms, which switch to vine growth habits in the shade[71].

Archaeobotanical investigation of VSO-bearing crops is relatively limited and reliant on a different range of techniques than commonly used for grains, fruits and nuts. Two microfossil techniques — phytolith and starch granule analysis, sometimes supplemented with raphide analysis — have been successfully applied to the identification of VSO-bearing plants in stratigraphic units (soils, sediments and deposits) at archaeological sites, as well as adhered to artefacts (stone and shell tools, pottery, and so on)[72-74]. Both microfossil techniques have limitations. Few of the most significant VSO-bearing crops produce phytoliths, produce phytoliths in sufficient quantity, or produce phytoliths with regular, diagnostic morphotypes to enable them to be useful for inferring domestication and cultivation in the archaeological record[72]. Starch granule research is plagued by methodological uncertainties in taphonomy of starch preservation, the ascription of taxonomic inferences, especially in the differentiation of wild and domesticated plants, and a lack of extensive reference collections for comparative analysis — although standardisation in the description and classification of starch morphotypes is advancing.

The preservation of charred, desiccated or waterlogged fragments of parenchyma derived from the VSO, as well as potentially other plant parts, has the greatest potential to inform our understanding of the exploitation, cultivation and domestication of VSO-bearing plants in the past. However, this type of archaeobotanical material is often highly fragmentary and lacking clear diagnostic features, making it extremely difficult to identify to organ type, let alone to genus and species taxonomic levels[75-77] or to differentiate wild versus domesticated forms[78,79]. The technical expertise to identify these plant types is still being developed encompassing optical and electron microscopy[77] and microCT[78-80]. As a result of conceptual and methodological problems, in most cases, we only know that a certain plant — sometimes identified to taxon, more usually an organography differentiating VSO-type (e.g., tuber, rhizome, corm, bulb) — was used by people at a certain site and date. No case study has yet been able to chart the domestication of a VSO-bearing plants through time using

archeobotanical evidence, although cultivation has been inferred, as in the case study of the Casma Valley, Peru[81–84].

In recent decades, the application of molecular techniques to archaeological materials — especially aDNA and mass spectrometry — has contributed greatly to our understanding of animal–human and plant–human interactions in the past. The application of these techniques to VSO-bearing crops has thus far not yielded significant results for understanding domesticatory processes, yet they have great potential to shed light on the domestication and dispersal of VSO-bearing crops through the molecular analysis of residues on artefacts, sediments and plaque accumulated on animal and human teeth.

Given the lack of a clear understanding of the phenotypic expression, rate and location of early domestication for any VSO-bearing crop in the past, we can only speculate on the mode of selection regime that characterised this process (Figure 2B). Currently, our understanding of the domestication histories for VSO-bearing crops is largely inferred from genetic studies of modern populations of cultivated and/or wild plants, such as manioc, potato, sweet potato, taro and yams[21]. Genetic studies, though, shed only limited light on the human practices entailed in plant domestication, namely the 'how, where and when' people cultivated, selected and moved plants.

Due to the high levels of phenotypic plasticity exhibited by many VSOs within different growth environments — visible at whole-organ and microscopic scales, as well as in phytochemistry[78,85] — people likely initially started controlling phenotypes through clonal propagation and management of growth environments. Asexual, or clonal propagation enables more direct phenotypic control for desired characteristics, such as flavour, colour, palatability, and so on; it is also necessary when plants are moved to new environments in which sexual reproduction is not viable, and also following the generation of sterile forms, most notably triploids. Plastic adaptation of vegetatively propagated plants to growth environments, including soil conditions and cultivation practices, was the primary driver of phenotypic variation and eventually led to the human-mediated clonal selection of new, domesticated forms.

From a genetic perspective, the domestication histories of VSOs represent an increasing shift from sexual recombination towards clonality, as vegetative propagation under cultivation became dominant. For instance, even though greater yam (*D. alata*) only reproduces asexually today, sexual reproduction has been inferred to have occurred in the deep past[86]. Most VSO-bearing crops, though, have retained sexual reproductive capacity, albeit a minor contributor to propagation and the resultant phenotypic and genotypic variation in populations under intensive human management. For example, sweet potato is vegetatively propagated under cultivation, has been moved outside its natural range and has no wild-type, yet new sexually derived progeny still spontaneously occur in cultivated plots and among feral stands, and are then incorporated into clonally reproduced stock[69,87]. The phylohistories for these VSOs represent the complex interplay of gene flow through sexual reproduction and clonal variation resulting from extended vegetative propagation (especially once taken to new environments in which a plant is no longer able to reproduce sexually).

In general, the contrasts between vegecultural crops and seed crops highlights the divergent pathways to plant domestication under different types of agricultural practices that need to be understood in their own terms (Figure 2C). Grouping crops with similar characteristics in terms of how they reproduce and domestication traits is a powerful means of building hypotheses about shared underlying processes. Recently, seven pathways have been hypothesized[22]: these include tuber and grain pathways, and also the domestication of camp-

following weeds, or ruderals, including many cucurbits — from *Curcurbita* in the Neotropics or North America to *Citrullus* in Africa. These species have been revealed archaeologically to be among the earliest plant domesticates in all three regions[88,89]. These domesticated plants complemented foraging economies rather than establishing agricultural economies. There were also a number of directed pathways, in the sense that these were new crops domesticated by societies with established agriculture. These included the domestication of perennial fruit trees and vines, which show a number of parallel evolutionary trends and were often important to more complex and urbanizing societies[90]. Another directed pathway saw established arable weeds (segetals), like oats (*Avena* spp.), Indian kodo millet (*Paspalum scrobiculatum*), or west African fonio millets (*Digitaria* spp.), transition from parasitic domesticoids to foci of production, and become domesticated more quickly. Archaeological evidence suggests these domestications were much more recent, often only 2000 or 3000 years ago[22]. A third directed pathway was where new crops, and major new varieties of crops, were selected for a particular purpose, such as the domestication of crops for fibre uses, from jute (*Chorchorus* spp.) and ramie (*Boehmeria nivea*) to cotton (*Gossypium* spp.), or the creation of fibre-adapted varieties, as happened in flax (*Linum usitatissimum*) and hemp (*Cannabis sativa*).

These pathways can be contrasted in terms of the extent to which they worked within a near natural habitat or were transplanted to more highly anthropogenic habitats (Figure 3; Table 2). Ecosystem engineering represents a pathway whereby domestication occurs within the ecological environment; as such, it is often useful to characterise these processes in terms of what some authors refer to as landscape domestication[91,92]: environments are managed to promote key species, such as useful trees, instead of being cleared for planting, such as hill sago palms (*Eugeissona utilis* and other species) on Borneo, swamp sago (*Metroxylon sagu*) in lowland New Guinea, or African oil palms (*Elaeis guineensis*), which are seen to expand in regional pollen data alongside new patterns of human settlement[31,93,94]. In this context, the rates and degrees of morphological change in the managed species may be limited or highly variable. Such landscape domestication may lead onto the other pathways for specific species. In the other pathways, there is an increasing removal of the focal species from their ecological environment or original, more limited biogeographic range — their removal may take place into a spectrum of anthropic growth environments from managed patch, to polycultural plot and field, to monocultural field.

Geographies of domestication and mosaics of evolution

The theoretical framework of the geographical origins of domesticated plants has developed through three principal phases over the past decade. Classically, geographic origins of domesticates have been correlated with Vavilov's system of centres of origin which identify regions of highest genetic diversity across multiple species as the most likely general source areas. Originally, eight such centres were identified around the globe, each associated with a 'cradle of agriculture' in North and South America, the Mediterranean, Near East, Northeast Africa, Central and Southern Asia and China[62,95]. Later, this system was expanded to include another centre in the Island Southeast Asia to New Guinea region, while the original centres were subdivided to reflect their multi-nucleated nature to give a total of between 13 and 24 geographic centres of origin (Figure 4)[96]. These centres of domesticated plant diversity typically, but not exclusively, map to regions of general high biodiversity suggestive of natural ancient cornucopias from which agriculture might spring. Naturally, this framework is suggestive of a system in which epicentres occur, and by extension, multiple localities and peoples were responsible.

Second, an asynchrony of domestication occurred across 'centres of origin' globally, with domesticated forms first appearing in western Asia between 11,000 and 12,000 years ago (9000 to 10000 BC), but the majority of domesticated forms appearing in the mid-Holocene between 6000 and 2000 BC in South Asia, Africa and the Americas[88]. In this second phase of development of the theoretical framework, it was increasingly recognized that complexity occurs even within putative centres. Although many species may originate from the same super-region, different species within that region appear to originate at different times and in different places, belying the concept of a single geographical and temporal point of origin. This is observed in all the early crops of the Near East[13], also in China[13,40], South Asia and in the Americas[88,97]. Even for single species in a single region, instances of the same crop originating at different times and places such as in the case of beans[98], chili peppers[99] and bananas[100]. It is therefore apparent that each regional centre was host to a number of processes over a wide geographical area. This level of complexity is further increased at the genome level, where a similar signal of something happening at a scale across the landscape occurs. Cereals such as barley[101] and emmer[102,103] show a mosaicism in their genomes, which indicates a contribution of wild ecotypes from across the geographical range, signifying a genetic departure from a long-lived assumption (or 'dogma') of a core area of origin[104]. Similarly, maize in North and South America show differences in their origins from the wild biogeographic range in Mesoamerica[25]. Recent work on bananas indicates major cultivar groups arose from a mosaic of different species, sub-species and cultivars across the New Guinea–Southeast Asian region[105]. Together, a picture is emerging of a process of origin which is inclusive of an entire landscape or region rather than just focal 'centres'[64,70].

The third and most incipient phase of developing a new framework concerns the mechanisms and processes behind a landscape level-process (Figure 5). While the original model of centres of origin implied relatively strong selection pressures and rapid processes involving necessarily severely bottlenecked populations[42,106], empirical evidence across many crops around the world generally indicates the opposite to be true[64,105]. As already noted, archaeobotanical evidence points to slow processes and necessarily low selection pressures, reminiscent of natural selection[18]. This protracted process undermines the notion of simple domestication 'events' that could be conceived in terms of single phylogenetic events[107], or in terms of a single bottleneck process: so far, the ancient genomic data from barley, maize and sorghum has not indicated a single, strong domestication bottleneck[108]. These selection pressures were dynamic, with changing behaviours and technologies, and likely had initially very low levels of selection extending back in time to over ten millennia before the onset of the earliest domesticated forms in the Near East, and as much as five millennia in China[37]. Contributing to slow processes of genetic change in crops, but also promoting human management of species, were degrees of phenotypic plasticity in many wild progenitors — in recent years, a growing number of studies have explored the potential for plastic responses to anthropic conditions to establish baselines from which domestication pathways proceeded[109,110]. Such long-term processes are suggestive of natural ecologies disturbed by human actions that have yet to be fully understood, and which preceded systematic cultivation, but from which the alleles of domesticated forms emerged. Such a scenario moves the framework of debate beyond whether domestication was conscious or unconscious into a realm in which it is not clear whether domestication was always even progressive in terms of food security.

Correlations of climatic records with radiocarbon records over time in the Near East indicate a dependence of population size on climate in the Late Pleistocene to early Holocene during the emergence of agriculture that did not decouple, indicating an independence of human demography from food security, until the Bronze Age, around 3300–1200 BC[111].

Intriguingly, by this time the nature of agricultural production had shifted from one that was labour-intensive and labour-limited to one that was more extensive and land-limited[112]. Similarly, in North America, agricultural populations were more constrained by climatic factors than contemporaneous hunter-gatherer populations[113]. In this emergent scenario, long-term human ecology appears to have had an impact on the ecosystem that resulted in adaptations by plants that did not immediately lead to an increased stability of human populations, and in fact may have had the opposite effect. In this framework, the density of human populations relative to the carrying capacity of the environment becomes significant and suggests the existence of tipping points that could be important steps in processes that sometimes promote domestication. Further recent evidence of these deep time periods is revealing long distance networks of human communication and exchange in the Epipalaeolithic of the Near East[114] and likely also in Late Pleistocene of China[115]. Together, the strands of recent evidence paint a picture of tipping points in human–environment and social (human–human) interactions, associated with increasing scales and densities of human communities, which steer towards pathways that ultimately lead to domestication of resources within landscapes and regions. In this framework, it becomes clearer why different geographic localities in the world experienced the rise of domestication at different times, as an ecological function of the carrying capacity relative to human density that differed across environments, affected to varying degrees by climatic factors and social processes.

Carrying capacity was also crucial in another way: it modulated the rates at which farming peoples spread by migration to new regions. Crops with higher productivity tend to allow for higher population density. By contrast, where productivity was lower human population would have approached 'notional' carrying capacity more frequently, promoting group fission and outward migration[116,117]. This is 'notional' in the sense that carrying capacity is an idealised concept relative to environment; tools, crops and cultivation practices; and, labour inputs relative to unit area of land. As a result, the early distribution of domesticates varies in part based on antiquity — those species that were domesticated earlier had more time to spread — and on productivity — those crops that were less productive were more susceptible to faster geographic spread.

An important axis of variation across world centres of domestication is that some were expansive, from which domesticated crops dispersed to much larger geographies — such as the spread rice from China, maize from Mesoamerica, pearl millet from west Africa, or wheat and barley from the Near East. By contrast, other crops remained quite local, such as Indian millets like *Brachiaria ramosa,* or many highland crops from Ethiopia and the Andes. The historically contingent processes behind the early translocation of domesticates means the productive potential of many crops may yet be realized by moving crops to regions that they had not been dispersed to in the past.

Futures of domestication research

Domestication processes have come to be better documented and understood in recent years. Along with these new insights into protracted and geographically dispersed processes of domestication have come many new questions, especially around how crops that followed different pathways were domesticated.

The slow process of domestication allowed a level of complexity in selection and the incorporation of genetic diversity that contrasts with the approaches of modern breeding. A combination of environmental and competitive selection allowed the fixation of alleles of large effect, possibly increasing trait heritability, without the removal of the rich diversity of alleles

of small effect through selection bottlenecks, as may be expected under a modern breeding approach. In this way, the transition to domesticated forms may have created a long-term stability that could not have been achieved through selective breeding. There may be a lesson for modern agriculture in terms of the resilience of diversity. One of the implications of genetic data is that crop success has come through processes of hybridity that create resilience. The multiple wild populations that have contributed to the genetic makeup of crop populations may be part of what made some crops, like bananas, barley, emmer and maize, long-term successes, by originally providing flexibility and diversity. It is clear that isolation over time erodes diversity and resilience, indicated, for example, in ancient genomes of sorghum from Nubia that document increase in genetic load over time, as well as genetic rescue through the introduction of new populations of sorghum from elsewhere[25].

Differences in the antiquity and productivity of crops resulted in some spreading rapidly or widely in the initial establishment of agriculture, while others did not, such as Ethiopian enset (*Ensete ventricosum*)[118], Andean oca (*Oxalis tuberosa*)[119], or Indian *Brachiaria ramosa* millet[120]. Some of these 'orphaned' and under-studied crops may well have considerable agronomic potential, and their study can only add to potential diversity and flexibility in future agricultural systems. One of the major questions that remains unanswered is why some crops that spread widely in the past retreated into oblivion. For example, *Triticum timopheevi* was a major crop in parts of Turkey before 6000 BC, spread from central Europe to Turkmenistan in the Neolithic, yet retreated in Bronze Age times, such that its historical distribution in the 20th century was restricted to Georgia[121,122]. The expanding research on domestication through archaeology and genetics is bringing forward a new period of insights into not just domestication processes, but the long-term sustainability and resilience of agriculture and different combinations of crops. Rather than seeing modern agriculture as a key to reconstructing the past, we can suggest that the past may play an increasingly important role in restructuring present agriculture for the future.

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Figure 1. Timeline of archaeobotanical evidence for morphological change in a selection of seed crops.

Assemblage data are plotted against median age (calibrated years BC). Upper graph charts percent of non-shattering. Lower graphs plots percentage change in mean grain size over the lowest value in the dataset for a dozen selected crops. Data taken from previous work[13,14,36,40], and augmented.

Figure 2. Comparisons of seed and tuber domestication pathways.

Schematic diagrams contrasting stages in the domestication process for (A) grains and (B) tubers, as well as (C) commonalities in terms of associated agroecosystems. (A) and (B) reprinted from Fuller *et al.*[22], with permission from the MIT Press.

Figure 3. Schematic representation comparing the seven pathways to plant domestication.
Interpretative emphases highlight the increasing degree of separation of species from environment (from ecosystem engineering, to ruderal, to tuber, to grain), as well as the greater directed selection in later pathways based on pre-existing cultivation practices (segetal, fibre and fruit tree).

Figure 4. Distribution of domestication pathways across centres of origin.

Map of recognized centres of domestication with selection of crops from each indicated in terms of domestication pathways, as defined in this paper. Some crops not derived from primary centres of origin are also indicated. Centres are based on Larson *et al.*[88] and updated here.

Figure 5. Maps demonstrating the landscape and regional frameworks for understanding the domestication of (upper) emmer wheat and barley (*Triticum turgidum* and *Hordeum vulgare*, respectively) and (lower) bananas (*Musa* cvs.).

In the upper diagram, the wild populations of both cereals are widely dispersed relative to the loci of domestication derived from archaeobotanical evidence. In the lower diagram, the source regions for AAB triploid domesticates (P = plantain; MP = *maoli-popo`ulu*) result from the anthropic movement of *Musa balbisiana* from Southeast Asia and *Musa acuminata* ssp. *banksii* from the circum-New Guinea region into contact zones. Image in lower panel reproduced from[70] with permission of Oxford Publishing Limited through PLSclear.

Table 1. Primary domestication traits in cereals (sexually reproduced) compared to domestication tendencies in VSOs (vegetatively propagated root crops) (extracted and modified from Denham *et al.*[21]: Table 2). While reproduction may be predominantly sexual or asexual for a given crop under cultivation, many crop taxa are able to reproduce using both modes of reproduction.

Category	Domestication trait in cereals	Domestication tendency in VSOs
Mode of reproduction	1. Partial or complete loss of asexual reproduction ability 2. Increased uniformity in seed germination traits; loss of dormancy	1. Partial or complete loss of sexual reproduction ability 2. Increased uniformity in clonal reproduction traits
Plant life cycle	Shift towards annual lifecycle based on sexual reproduction from seed	Shift towards perennial lifecycle based on vegetative production of suckers, shoots, underground storage organs and other viable plant parts
Yield of edible portion	1. Increased size in seeds of cereals, legumes, nuts, stone fruits 2. Increased number of fruits and seeds 3. Increased ratio of edible to non-edible plant parts in whole plant	1. Increased size of edible vegetative storage organs (often the organ used for clonal propagation) 2. Increased number of edible organs 3. Increased ratio of edible to non-edible plant parts in whole plant.
Ease of harvesting	Development of non-shattering seed heads/pods	Development of bunched or fused vegetative storage organs Development of easily separated VSOs/bud separation
Timing of production	Synchronous production of harvested parts within plant and between plants	Asynchronous and more continuous production of harvested parts, with effectively in-ground storage for some VSOs
Plant architecture	Changes in: Apical dominance Branch arrangements Leaf arrangements	Changes in: Apical dominance Branch arrangements Leaf arrangements
Defensive adaptations	Loss of defensive adaptations (spines, hard seed casings, toxicity, acridity) to enhance harvesting, processing and consumption	General loss of defensive adaptations (spines, hard seed casings, toxicity, acridity) to enhance harvesting, processing and consumption

Ancillary/improvement/diversification/dispersal		
Ease of storage	1. Traits that favour survival of seeds used for propagation 2. Traits that favour preservation of seeds used for consumption	1. Traits that favour survival of VSOs used for propagation 2. Traits that favour preservation of VSOs used for consumption
Photoperiod sensitivity	Changes in photoperiod sensitivity according to latitude, reproductive cycle of the wildtype, and latitudinal origin of wildtype	Changes in photoperiod sensitivity according to latitude and reproductive cycle of the wildtype, and latitudinal origin of wildtype
Environmental tolerance	Traits that enable cultivation in wider environmental range (altitudinal, latitudinal, water conditions, wind conditions, and soil type)	Traits that enable cultivation in wider environmental range (altitudinal, latitudinal, water conditions, wind conditions, and soil type)
Disease resistance	Reduced resistance to disease and pests due to human selection following continued sexual reproduction of sub-population	Dramatic reduction in resistance to disease and pests due to low genetic variability in clonally reproduced cultivars (despite somatic mutation)
Palatability	Selection for various desired traits, often involving a loss of defensive chemical adaptations	Selection for various desired traits, often involving a loss of defensive chemical adaptations
Processing	Selection for reduction or ease of removal of inedible portions (free-threshing cereals, seed integument, nutshells, pod shells)	Selection for reduction or ease of removal of inedible portions (skin, fibre)

Table 2. Pathways to plant domestication. These pathways are not exclusive, rather they represent commonalities in the ways that plants were domesticated by people in different parts of the world in the past.

Pathway	Description	Example crops
Ecosystem engineering	Focus on long-lived trees, palms and pandanus within managed ecosystems	Brazil nut (*Bertholletia excelsa*) Oil palm (*Elaeis guineensis*) Pandans (*Pandanus conoideus/julianettii*) Sago palm (*Metroxylon sagu*) Enset (*Ensete ventricosum*)
Ruderal	Plants that adapt and spread within disturbed, anthropic environments, such as camp-following commensals; need not initially be associated with cultivation in plots/fields	Bottle gourd (*Lagenaria siceraria*) Cane grasses (*Saccharum* spp.) Chili peppers (*Capsicum* spp.) Squash (*Cucurbita* spp.)
Tuber	Plants that yield starch-rich underground storage organs that are reproductively viable and can be used for vegetative propagation of the crop	Manioc/cassava (*Manihot esculenta*) Potato (*Solanum tuberosum*) Sweet potato (*Ipomoea batatas*) Taro (*Colocasia esculenta*) Yams (*Dioscorea* spp.)
Grain	Annual crops grown for/from seeds (especially cereals and pulses)	Barley (*Hordeum vulgare*) Lentil (*Lens culinaris*) Pea (*Pisum sativum*) Wheat (*Triticum* spp.) Rice (*Oryza sativa*) Soybean (*Glycine max*) Maize (*Zea mays*)
Segetal	Former weedy species that grew in agricultural contexts that were added to the crop repertoire (and also important for fodder)	Indian kodo millet (*Paspalum scrobiculatum*) Oats (*Avena sativa*) Rye (*Secale cereale*) West Africa fonios (*Digitaria exilis, D. iburua*)
Fibre	Directed selection of species that were already crops or weeds, but subsequently grown for fibre and not food	Cotton (*Gossypium* spp.) Flax (*Linum usitatissimum*) Hemp (*Cannabis sativa*) Jute (*Chorchorus* spp.)

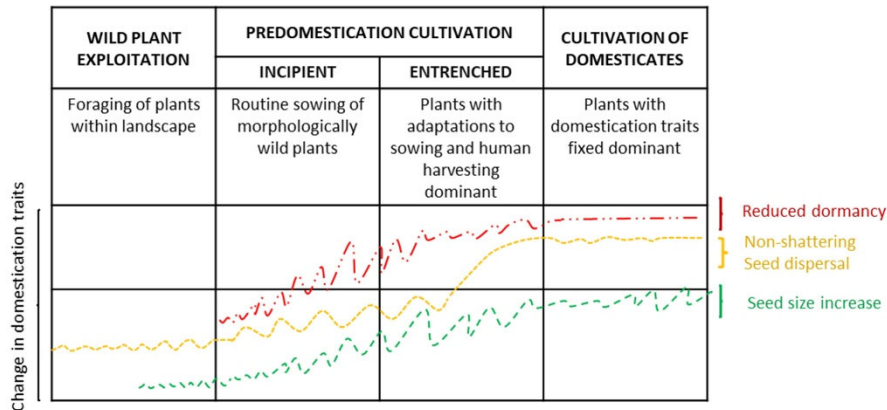|		
Fruit tree	Woody, longer-lived perennial species grown for fruit that are added to existing grain or tuber-based economies; initially planted from seed (often for an extended period) and then often propagated using cuttings/grafting/vegetatively	Citrus (*Citrus* spp.) Date palm (*Phoenix dactylifera*) Fig (*Ficus carica*) Grape (*Vitis vinifera*) Olive (*Olea europaea*) Peach (*Amygdalus persicus*) Avocado (*Persea americana*)

In Brief

Crop domestication occurred across dozens of regions, over thousands of years. Fuller et al. review how archaeobotany and genetics are revealing roles for adaptive selection, phenotypic plasticity, and regional patterns of gene flow that enhanced diversity facilitated by cultural networks of interaction. **(au: I needed to shorten this a little – is this ok?)**
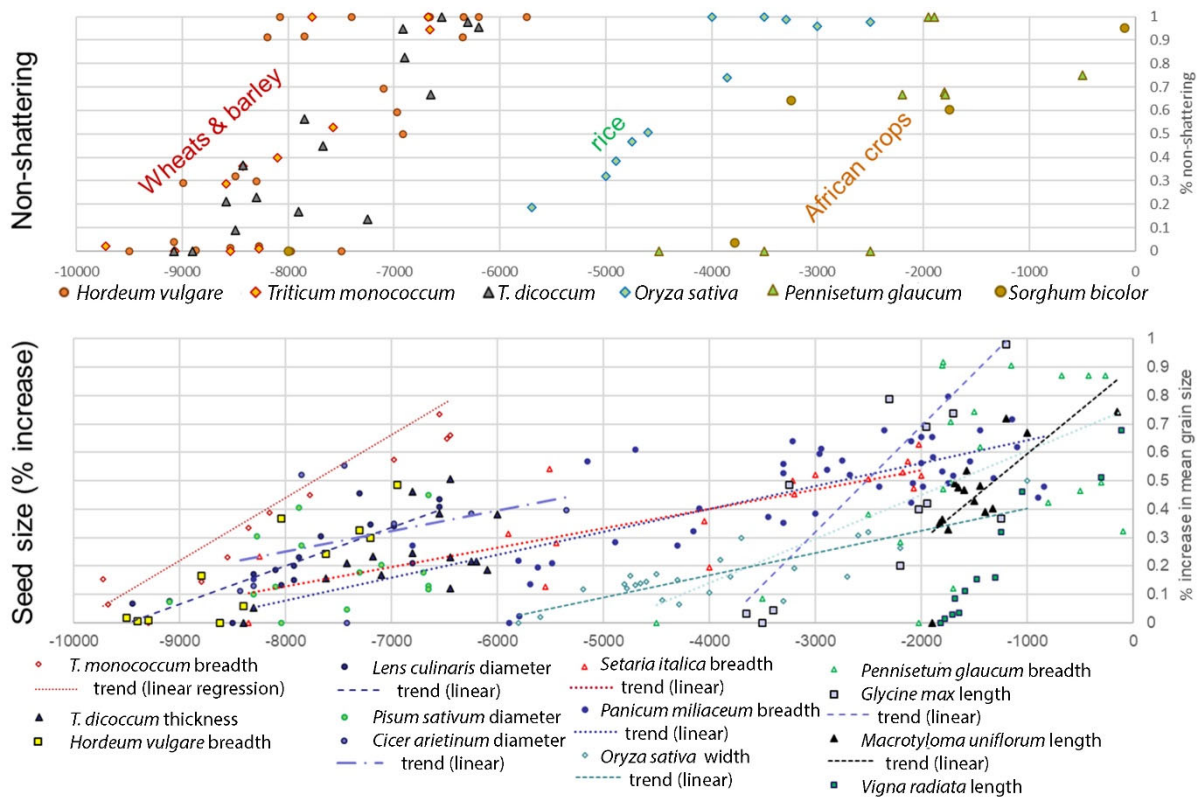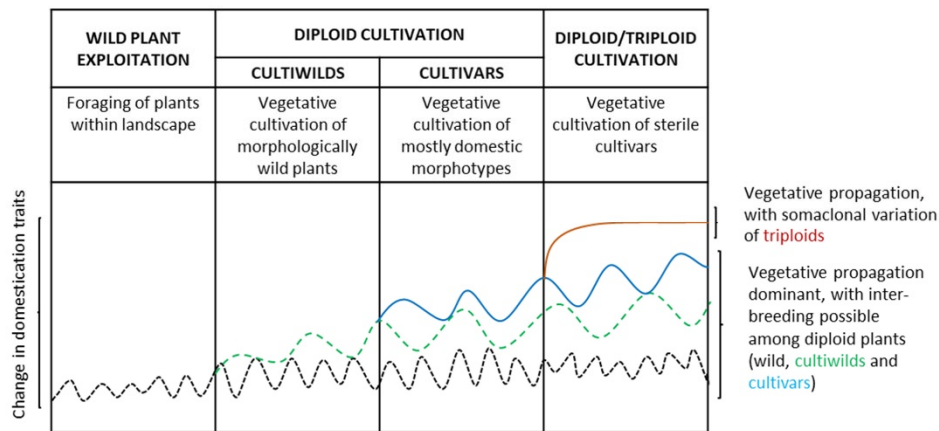
Fig. 1 Archaeobotanical data plotting changes in percentage shattering (upper) and grain size (lower) through time for barley (*Hordeum vulgare*), einkorn wheat (*Triticum monococcum*), emmer wheat (*Triticum turgidum*), and East Asian rice (*Oryza sativa*). The key data points for both domestication traits that mark the duration of the domestication episode for each species are presented. Source: Fuller et al. 2014: Fig. 1 (*to be amended slightly for final version*)

a) Grain pathway

WILD PLANT EXPLOITATION	PREDOMESTICATION CULTIVATION		CULTIVATION OF DOMESTICATES
	INCIPIENT	ENTRENCHED	
Foraging of plants within landscape	Routine sowing of morphologically wild plants	Plants with adaptations to sowing and human harvesting dominant	Plants with domestication traits fixed dominant

Change in domestication traits

- Reduced dormancy
- Non-shattering Seed dispersal
- Seed size increase

b) Tuber pathway

WILD PLANT EXPLOITATION	DIPLOID CULTIVATION		DIPLOID/TRIPLOID CULTIVATION
	CULTIWILDS	CULTIVARS	
Foraging of plants within landscape	Vegetative cultivation of morphologically wild plants	Vegetative cultivation of mostly domestic morphotypes	Vegetative cultivation of sterile cultivars

Change in domestication traits

Vegetative propagation, with somaclonal variation of triploids

Vegetative propagation dominant, with inter-breeding possible among diploid plants (wild, cultiwilds and cultivars)

c) Commonalities between pathways

Exploitation within natural range	Exploitation/cultivation within/near natural range	Limited dispersal to new ecozones beyond natural range	Widespread dispersal into diversified ecozones
Wild plants	Increased diversity of morphologically wild types under management and cultivation	Accumulation of crop diversity	Dominance of few varieties despite varietal diversification
Management of plants within environment	Managed patch-based exploitation, small-scale plot cultivation	Plot and field-based cultivation dominant	Plot and field-based cultivation dominant
Limited impact on environment	Human modified environments near occupation areas	Intensive degradation of local environments	Extensive degradation of environments on regional scale
Increasing returns per unit of time		Increasing returns per unit of land	

Fig. 2 Schematic diagrams contrasting stages in the domestication process for (a) grains and (b) tubers, as well as (c) commonalities in terms of associated agroecosystems. Source: Fuller and Denham 2022: Figs. 10.3 and 10.7, which are updated and augmented here.
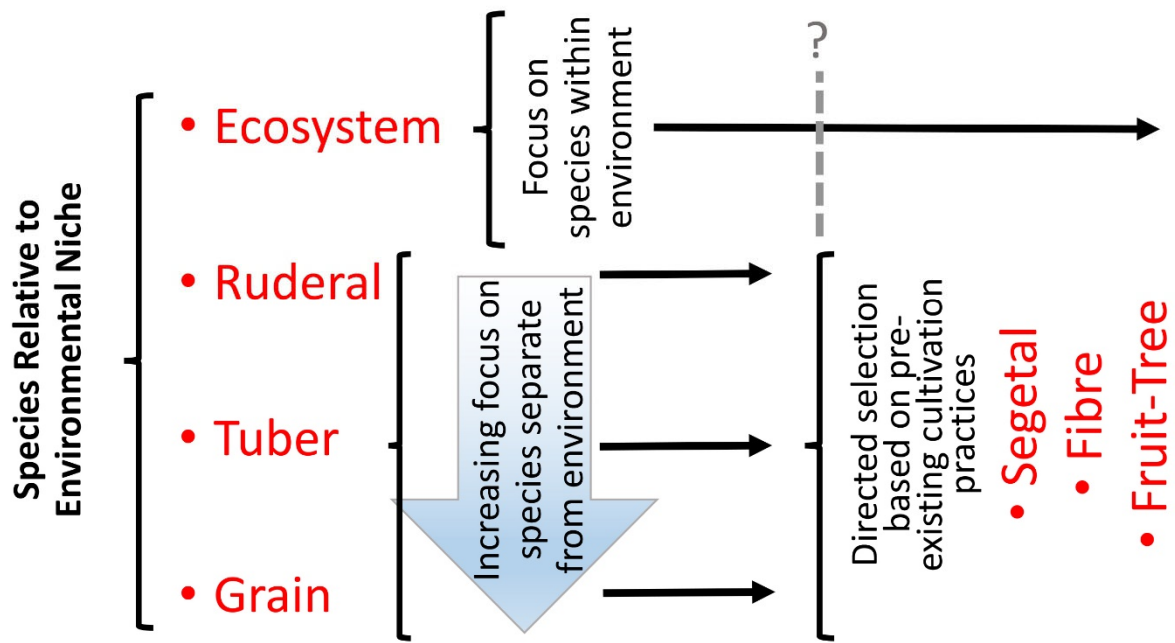
Fig. 3 Schematic representation comparing the seven pathways to plant domestication. Interpretative emphases highlight the increasing degree of separation of species from environment (from ecosystem engineering, to ruderal, to tuber, to grain), as well as the greater directed selection in later pathways based on pre-existing cultivation practices (segetal, fibre and fruit tree). Source: Tim Denham and Dorian Fuller
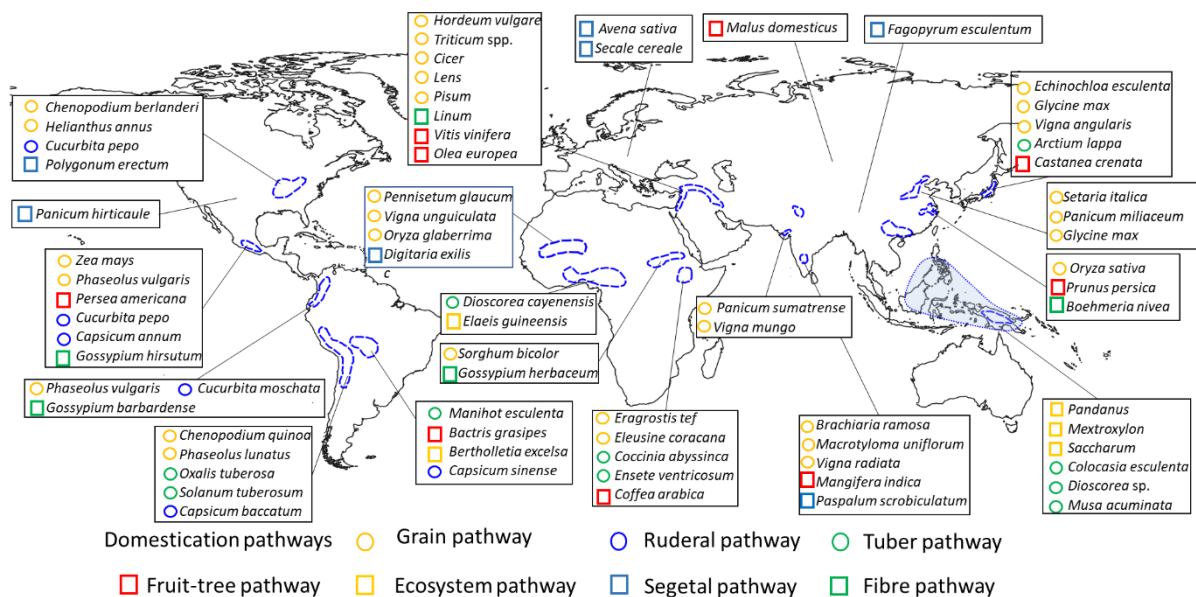
Fig. 4. World map showing decentred loci of domestication for globally significant food crops grown in fields (monoculture) and plots (polyculture). Loci are shaded to indicate whether domestication occurred in the early (c. 12,000-8000 BP) or middle (c. 8000-4000 BP) Holocene. Domesticatory disposition indicates broad regions across which people likely shared orientations and practices of cultivation, although the actual archaeological evidence for domestication for particular species is more limited. Groups of crops are colour-coded according to: sexually reproduced cereals (blue); sexually reproduced legumes and vegetables (green); and vegetatively propagated bananas, root crops and sugarcane (orange). Arboricultural/silvicultural crops, such as trees, palms and pandanus, as well

as fodder and fibre crops are excluded. An asterisk connotes that plants probably moved as a weed from the region of origin to be domesticated in another locale (segetal pathway); oats (*Avena sativa*) and rye (*Secale cereale*) originated in South-west Asia and were probably domesticated in eastern-central Europe during the late Holocene. Loci of domestication Source: Denham et al. 2020: Fig. 1 (upper).
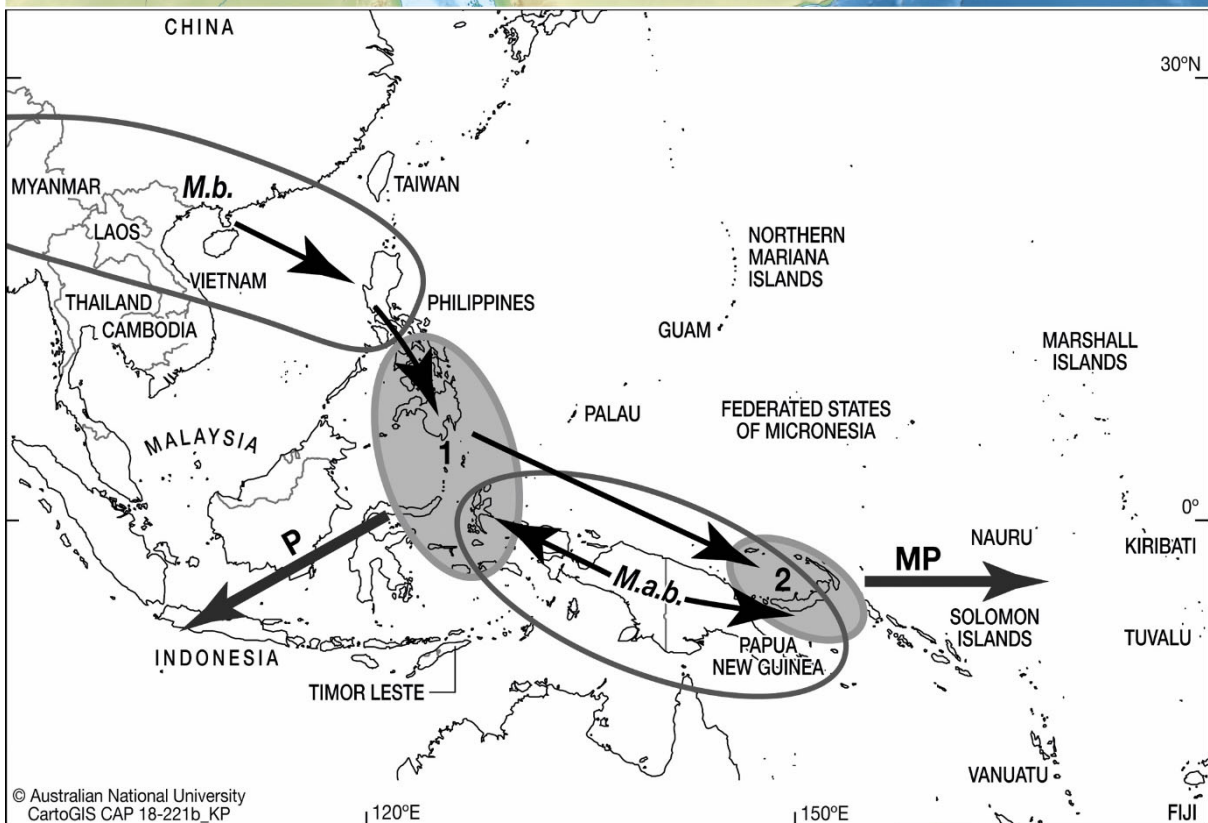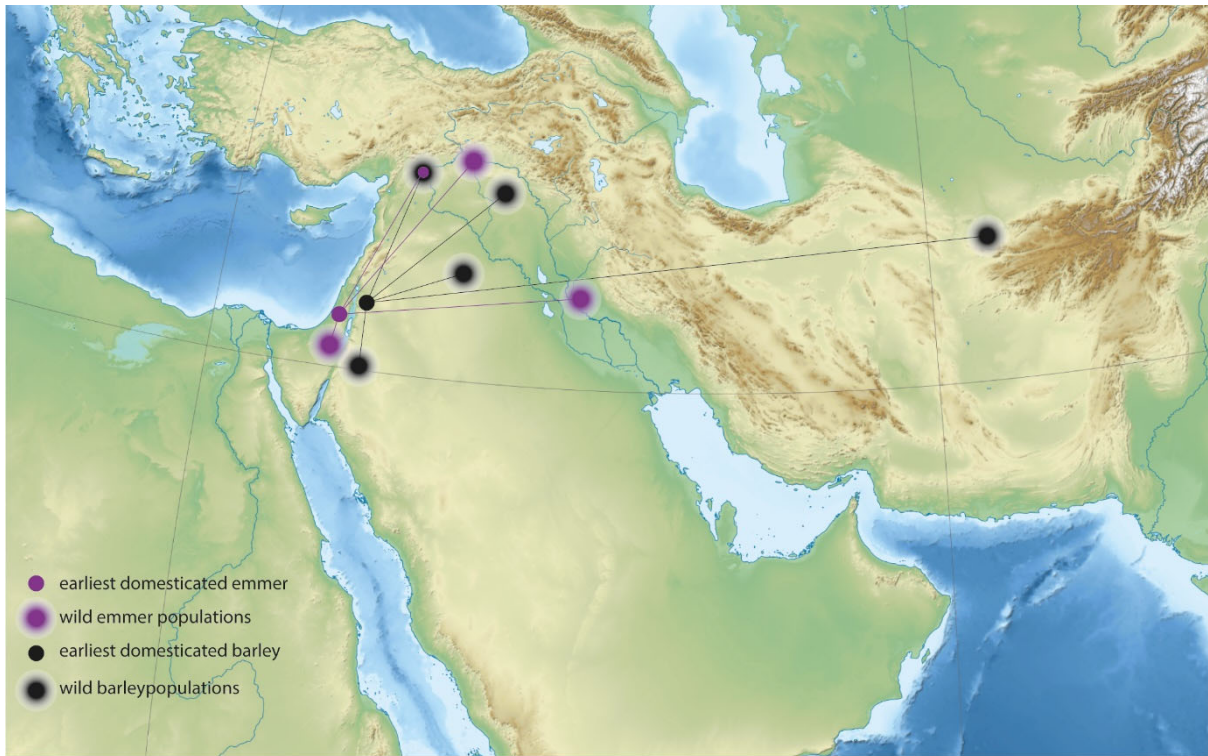
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		Jute (*Chorchorus* spp.)
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