Far from the Hearth
Essays in Honour of Martin K. Jones

Edited by Emma Lightfoot, Xinyi Liu & Dorian Q Fuller
Far from the Hearth
(Above) Martin Jones at West Stow, 1972 (with thanks to Ian Alister, Lucy Walker, Leonie Walker, and West Stow Environmental Archaeology Group); (Below) Martin Jones in a millet field, Inner Mongolia, 2010. (Photograph: X. Liu.)
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Acknowledgements

The initial idea of editing this volume grew out of a conversation between Xinyi Liu and Graeme Barker at St John’s College, Cambridge in June 2016. The editors subsequently discussed the provisional layout of the volume. By April of the following year, our list of agreed contributors was complete. Abstracts followed, and the chapters themselves soon after. First of all, the editors would like to pay tribute to our 36 authors, whose excellent work and timely contributions made it all possible.

For the last two-and-a-half years, the volume has been known as ‘Fantastic Beasts’ in order to keep it a secret from Martin. As we enter the final stage, we wish to extend our thanks to all who have ensured Martin remains blissfully unaware, including Lucy Walker, and we offer her our sincere thanks. We are extremely grateful to Harriet Hunt, Diane Lister, Cynthia Larbey and Tamsin O’Connell, who are kindly organizing the gatherings to mark Martin’s retirement and the publication of this volume.

With respect to the volume’s production, we would like to thank the McDonald Institute for Archaeology Research for financial support. The McDonald Monograph Series Editor James Barrett oversaw and encouraged all aspects of this project, and we offer him sincere thanks. We would also like to acknowledge the support of Cyprian Broodbank, not least for allowing us to host the workshop at the institute, but also for his encouragement throughout all phases of the volume’s implementation. Particular thanks must go to several key individuals: Anne Chippindale, Ben Plumridge, Emma Jarman, Simon Stoddart and Samantha Leggett. Finally, we are also grateful to the anonymous reviewers who recommended changes that have greatly enhanced the final version of this volume.

Xinyi Liu, Emma Lightfoot and Dorian Fuller
August 2018
Foreword

The 28-year term of Martin Jones as the first George Pitt-Rivers Professor of Archaeological Science witnessed, and in part created, a transformation in the fields of environmental and biomolecular archaeology. In this volume, Martin’s colleagues and students explore the intellectual rewards of this transformation, in terms of methodological developments in archaeobotany, the efflorescence of biomolecular archaeology, the integration of biological and social perspectives, and the exploration of archaeobotanical themes on a global scale. These advances are worldwide, and Martin’s contributions can be traced through citation trails, the scholarly diaspora of the Pitt-Rivers Laboratory and (not least) the foundations laid by the Ancient Biomolecules Initiative of the Natural Environment Research Council (1989–1993), which he chaired and helped create. As outlined in Chapter 6, Martin’s subsequent role in the bioarchaeology programme of the Wellcome Trust (1996–2006) further consolidated what is now a central and increasingly rewarding component of archaeological inquiry. Subsequently, he has engaged with the European Research Council, as Principal Investigator of the Food Globalisation in Prehistory project and a Panel Chair for the Advanced Grant programme. As both practitioner and indefatigable campaigner, he has promoted the field in immeasurable ways, at critical junctures in the past and in on-going capacities as a research leader.

The accolades for Martin’s achievements are many, most recently Fellowship of the British Academy. Yet it is as a congenial, supportive—and demanding—force within the Pitt-Rivers Laboratory that the foundations of his intellectual influence were laid. Here, each Friday morning, the archaeological science community would draw sticks to decide who would deliver an impromptu research report or explore a topical theme. Martin is among the most laid-back colleagues I have worked with, yet simultaneously the most incisive in his constructive criticism. As a provider of internal peer-review he was fearless without being unkind. The themed Pitt-Rivers Christmas parties were equally impactful—on one occasion Alice Cooper appeared, looking ever so slightly like our professor of archaeological science.

Martin’s roles as a research leader extended to several stints as head of the Department of Archaeology, chairing the Faculty of Archaeology and Anthropology and serving as a long-term member of the Managing Committee of the McDonald Institute for Archaeological Research. Having started his professional career as an excavation-unit archaeobotanist in Oxford, he was a long-standing proponent of the highly successful Cambridge Archaeological Unit. In the wider collegiate community, he is a Fellow (and was Vice-Master) of Darwin College and was the staff treasurer of the Student Labour Club. In all roles he fought valiantly and often successfully for the interests of his constituency. His capacity to fight for deeply held priorities while recognizing the value of diverse perspectives was of utmost importance. His nostalgic enthusiasm for the debate with archaeological science that was engendered by the post-processual critique is one signal of an underlying appreciation of plurality. His active support for the recent merger of the Divisions of Archaeology and Biological Anthropology, within our new Department of Archaeology, is another. As a scientist (Martin’s first degree, at Cambridge, was in Natural Sciences) he values the peer-reviewed journal article above all scholarly outputs, yet has authored as many highly regarded books as a scholar in the humanities. His Feast: Why humans share food has been translated into several languages and won Food Book of the Year from the Guild of Food Writers. He views academia and society as a continuum, campaigning for archaeobotanical contributions to global food security (e.g. by promoting millet as a drought-resistant crop) and working with world players such as Unilever to encourage archaeologically informed decisions regarding food products.

That Martin’s achievements and influence merit celebration is clear. That his colleagues and students wish to honour him is equally so. Yet does the McDonald Conversations series publish Festschriften? This is a semantic question. As series editor I am delighted to introduce a collection of important papers regarding the past, present and future of archaeobotany, representing its methodological diversity and maturity. That this collection concurrently pays respect to a treasured colleague is a very pleasant serendipity.

Dr James H. Barrett
Chapter 15

The Geography of Crop Origins and Domestication: Changing Paradigms from Evolutionary Genetics

Harriet V. Hunt, Hugo R. Oliveira, Diane L. Lister, Andrew C. Clarke & Natalia A.S. Przelomska

Introduction

The question of single or multiple domestications is of enduring interest in the bioarchaeology of cultivated plants. It is considered by many as one of the key questions regarding domestication (e.g. Larson et al. 2014). The volume of attention devoted to this topic stems, in part, from its position at the interface of archaeology and evolutionary biology. It relates both to archaeological paradigms of socioeconomic revolution, technological innovation, contact and dispersal among human societies (Blumler 1992) and to the distinct evolutionary paradigms of adaptive novelty and speciation applicable to all biological taxa.

The biological question of the number of domestications (and implicitly, their locations in time and space) of crop plants is often a proxy for the archaeological question regarding the timing and location of the origins of agriculture. As such, as Harris (1990) and Langlie and colleagues (2014) have commented, researchers may find it hard to escape from the paradigm of ‘packages’ of crops that originated in distinct ‘centres of origin’ (Vavilov 1926; 1951), and often correlated with major ancient civilizations (cf. Langlie et al. 2014).

Vavilov both created the concept of centres of origin of crop plants and developed the first essentially genetic approach to inferring such centres. Since then, increasingly sophisticated genetic, genomic and statistical methods have driven successive paradigms for inferring the number and location of domestication ‘events’ (or ‘processes’, as discussed below). At the same time, the genomics revolution has opened up entire new areas for archaeogenetic research on domestication, such as the microevolutionary processes associated with domestication, the evolution of functional traits and epigenetics. Thus, the question of single versus multiple domestications, which dominated genetic research on domesticates in the late 1990s–early 2000s (Bruford et al. 2003; Salamini et al. 2002), is now just one line of enquiry. Thus, while the origins of an increasingly diverse suite of crops and other ethnobotanically important plant species have been interrogated using genetic data, the extent of the analysis underpinning current interpretations is highly variable. For some species, especially those of greatest modern economic importance, successive research projects have revised and honed interpretations through cutting-edge data and analytical methods. Meanwhile, the conclusions for other species are still inferred from genetic markers and statistical analysis whose known limitations are often not properly discussed. Moreover, although ‘domestication’ is a notoriously thorny concept to define, many studies do not adequately engage with the term, or address whether the given data can discriminate between different ‘domestication’ scenarios as they use it.

In this chapter, we review the development of thought on the inference of domestication geographies from genetic data, exploring how paradigms have shifted from the centres of origin concept developed by Vavilov. We review the debate over single versus multiple domestications, and the implications of protracted domestication and on-going gene flow for inferring the geography of domestication. Rather than provide a state-of-the-art for any one crop, or a comprehensive survey of the many crops whose origins have now been interrogated using genetic data, we use diverse crops to illustrate how varying analytical approaches and paradigms of domestication have shaped the debate.

‘Origins’ versus ‘domestication’

The vast literature on crop evolution refers to both ‘origin[s]’ and ‘domestication’ of plant species (in both cases frequently preceded by the phrase ‘centres of’). These terms are sometimes used synonymously, but
from a genetic point of view they represent different, but interrelated, evolutionary processes. ‘Domestication’ can be defined as a process of human-driven selection, resulting in the evolution of particular phenotypes adapted to cultivation and/or anthropogenic landscapes. These phenotypes include non-shattering seed-head habit, increased grain size, reduced branching, reduction of plant biochemical defences, loss of seed dormancy and more predictable germination (Harlan 1992). At the molecular level, this process entails the trajectory towards population fixation of domestic-type alleles, either from novel mutations or standing variation (Gepts 2014; Larson et al. 2014). In contrast, from a population genetics or phylogenetic perspective, ‘origins’ implies a process of reproductive isolation or phylogenetic bifurcation of the phenotypically wild from phenotypically domesticated taxon. These two processes may be linked by the evolutionary trajectory of reproductive trait genes, but they have their own respective suites of associated processes and drivers. This distinction has implications for localizing ‘origins’ and/or ‘domestication’ in time and space.

Vavilov, centres and diversity

The origins of particular crops (an evolutionary process) may or may not correlate with ‘agricultural origins’ as a human cultural behaviour. The conceptual link between the two originates largely from Vavilov (1926); as commented by Harris (1990), ‘Vavilov’s concept of centres of origin of cultivated plants has had such a profound effect on students of the beginnings of agriculture that it remains very difficult for anyone who takes a world view of agricultural origins to escape the mental template of the Vavilovian pattern of centres’. The connection with human prehistory is made in the concluding section of Vavilov (1926): ‘the elucidation of the centres of type-formation and the origin of cultivated plants allows us to approach objectively the establishment of basic foci of agricultural civilizations’ (Fig. 15.1).

Harris notes that ‘ever since Vavilov himself equated centres of crop diversity with the homelands of agriculture there has been conceptual confusion between the two phenomena’ and that ‘it is time that we conceptually decoupled the world pattern of crop-plant diversity that Vavilov so brilliantly demonstrated from our investigations of the origins and early development of agriculture’. In fact, Vavilov himself focuses strongly on crop ‘origins’ rather than ‘domestication’ or ‘agriculture’; his writings are concerned principally with the evolution of ‘types’ [cultivated plant varieties], and the role of human agency, and integration with archaeological evidence, are mentioned only in passing. The question of single versus multiple origins of a given crop was not explicitly raised by Vavilov, who appears to have assumed that each crop could only be associated with one geographical centre. However, Vavilov’s approach was an essential precursor to the debate of whether such origins were unique in geographical and phylogenetic space.

Vavilov’s principal assumption was that the geographic origins of each crop taxon co-localized with its highest genetic [=phenotypic] diversity. The theoretical underpinning of this idea shares intellectual links with Willis’ (1922) ‘age and area’ hypothesis on infrageneric diversity (see Hawkes 1983). Assuming a constant mutation rate and selection pressure, the evolution of diverse types or varieties would track the length of time a plant species had existed in a...
given region. To a modern evolutionary geneticist, a number of questions immediately present themselves: Vavilov’s theory explains the diversification of a crop species, but its origins from a wild ancestor remain nebulous. It is also unclear whether Vavilov imagined that diversity within a crop species arose by *de novo* mutation post-domestication, or was already present as standing variation in wild populations. This distinction is a key question in current research on adaptation genomics and domestication (Barrett & Schluter 2008; Ross-Ibarra et al. 2007). Vavilov’s assumptions also appear to foreshadow the neutral theory of molecular evolution and the molecular clock hypothesis (Kimura 1983) in relating accumulation of diversity to age of a lineage. Given Vavilov’s emphasis on phenotypic, adaptive traits, however, the downplaying of emphasis on the strength of diversifying selection, and its consequences for evolutionary rates, now appears problematic. The relative role of natural and anthropogenic diversifying selective forces is also little explored.

As studies of crop diversity moved into a molecular era unknown in Vavilov’s time, an increasingly rigorous quantitative and statistical framework developed. This complexified the task of identifying centres of variation. Even simple descriptive population genetics has at its disposal several statistics for quantifying genetic diversity in a region, which may give conflicting answers regarding maximum diversity. Moreover, the designation of geographical regions for comparison is inherently subjective, one driving factor behind the development of modelling approaches in which samples are treated as individuals rather than being pre-assigned to subjectively defined populations (Pritchard et al. 2000).

Vavilov himself was well aware that an observed centre of crop diversity did not necessarily represent the crop’s centre of origin, in particular considering hybridization with other wild species as a mechanism for generating secondary centres of diversity. He identified a number of other criteria by which centres of origin could be identified: the distribution of the wild ancestor; the presence of endemic forms; and high frequency of genetically dominant traits. Over his career, he revised the number of proposed centres from the initial five in 1926 to seven in his final synthesis published in 1940 (Vavilov 1940; Fig. 15.1). Subsequently, diverse authors from the Soviet Union, Britain, France and the USA proposed either additional centres, to as many as 16 (Darlington 1973), or as few as three (Harlan 1971, reviewed in Hawkes 1983 and Harris 1990). As noted by Hawkes, some of the disagreement comes down to the semantics of what constitutes a ‘centre’ and attempts to discriminate between ‘megacentres’ and ‘microcentres’. How large does a centre have to be, to be termed as such? Vavilov’s centres were identified at the broad continental scale, but how precisely can and should we attempt to localize the origins of crops? This question is tied up with determining single versus multiple domestications.

Vavilov’s concept continues to pervade thinking about agricultural origins and domestication, as explored by Harris (1990) and still true today. For example, Meyer and Purugganan (2013), in a statement that underplays the complexity of domestication, say ‘crop species are domesticated in particular locales’. The linking of elevated genetic diversity with ancestral populations remains a minor strand of population genetic interpretation, especially for under-resourced crops and those where the direct wild ancestor is uncertain. For example, Hu and colleagues (2009) proposed China’s Loess Plateau as the centre of origin of broomcorn millet (*Panicum miliaceum*) and Guo and colleagues (2014) inferred the classical Old World as the centre of origin of turnip rape (*Brassica rapa*), based on microsatellite diversity. However, while Vavilov’s concepts persist in the broad intellectual landscape of understanding the origins of agriculture, the evolutionary emphasis for individual crops shifted to tracing ancestor-descendant relationships and unpacking the evolution of particular loci.

**Phylogenetic methods to reconstruct crop domestication**

From the late 1950s, phylogenetic methods gained ground as a new framework for identifying crop domestication ‘events’. We put this term in quotation marks because it is frequently encountered in the early phylogenetic literature in particular, but (like ‘centres’) its usefulness is dependent on the temporal and spatial scale under consideration. As explained further below, both archaeobotanical and genetic evidence are now moving away from an ‘event’-like concept of domestication.

The growth of phylogenetics was associated with the development of computers and the introduction of algorithms for phylogenetic reconstruction, as well as advances in understanding the molecular mechanism of evolution which led to the availability of ‘direct’ genetic data in the form of protein, and later DNA, sequences (Felsenstein 2004). A phylogeny constitutes an explicit hypothesis about ancestor-descendant relationships, speaking directly to one of the core paradigms of domesticates as discrete taxa descended from other, wild ancestral taxa. Phylogenies represent evolution as a branching genealogy, in which extant lineages result from a series of bifurcations from a
common ancestor; the monophyly of a domesticated taxon relative to its wild progenitor is therefore interpreted as a single domestication. The development of phylogeographic methods in the late 1990s drove efforts to localize ‘domestication events’ in space, by identifying where those wild varieties that shared the most recent common ancestor with the domesticated lineages were located.

For a review of phylogenetic methods, readers are referred to one of the numerous reviews and standard texts (e.g. Bleidorn 2017; Felsenstein 2004; Salemi et al. 2009; Uncu et al. 2015). The number and choice of genetic markers can affect the inferred phylogeny. Many studies on single genes have resolved a monophyletic origin of crops, along with strong selective pressures under domestication, while those based on genome-wide data show evidence of multiple domestications (Fankin & von Korff 2017). Additionally, different phylogenetic methods can suggest different domestication histories.

Work on phylogenetic inference of crop plant domestication began with wheat, using ‘anonymous’ genetic markers such as Amplified Fragment Length Polymorphisms (AFLPs). Heun and colleagues (1997) analysed AFLPs in domesticated einkorn (T. monococcum subsp. monococcum) and its wild progenitor (T. monococcum subsp. aegilopoideus). All domesticated lines clustered together in a neighbour-joining tree, and their sister clade included wild accessions from only the Karaca Dağ Mountains in Turkey (fig. 2E in Heun et al. 1997). The authors concluded that einkorn was domesticated only once from wild einkorn in that region. The same approach applied to emmer wheat, based on AFLPs screened in domesticated lines (T. turdium subsp. dicoccum) and wild emmers (T. turdium subsp. dicoccoides), also found that the wild emmers closest phylogenetically to the cultivated clade were from the Karaca Dağ Mountains (fig. 1 in Özkan et al. 2002). This led many biologists and archaeologists to pinpoint southeast Turkey as the cradle of Near Eastern agriculture (Lev-Yadun et al. 2000).

Martin Jones and Terry Brown (M. Jones 2004; M. Jones & Brown 2000), synthesizing this first wave of phylogenetic crop domestication studies, noted the emerging consensus of single-origins conclusions for the major Old World crops inferred from monophyly of domesticated lineages. Maize followed the same pattern, in a major study based on microsatellites (Matsuoka et al. 2002). The phylogenies of all these crops were based on markers with no direct DNA sequence information. Patterns of similarity across many loci were compressed to pairwise genetic distance measures which are then used to construct phylogenetic trees using deterministic computer algorithms. However, inferences from biallelic markers (including AFLPs) were called into question by Allaby and Brown (2003), who used computer-simulated AFLP data to show that domesticated crops could appear monophyletic even when the true history was a multiple-origin, polyphyletic scenario. An on-going debate ensued on the validity of different phylogenetic methods and on the effect of pollination type, pace of domestication, selection and population parameters on phylogenetic trees (Allaby et al. 2008; 2010; Heun et al. 2008; 2012; Honke & Heun 2009; Ross-Ibarra & Galt 2008; Salamini et al. 2004). We return to these issues below.

Rice (Oryza sativa) has perhaps received more attention than any other crop with regard to debates on single versus multiple domestications. The extraordinary intensity of debate, including the volume of data and sophistication of models and computational methods, and frequent overturning of conclusions, can be attributed both to the parallel ferocity of archeobotanical debate on the trajectory(ies) to domesticated rice and the early sequencing of the rice genome (Goff et al. 2002; Yu et al. 2002). Oryza rufipogon is the wild ancestor of rice (O. sativa), but because this species is widespread throughout Asia it is unclear if the different rice varieties resulted from independent domestication events, or if rice was introduced from a single core area and gave rise to the different major varieties, indica and japonica, by local adaptation or by hybridization with native wild rice.

Phylogenetic analysis of DNA and protein sequences of rice domestication loci, controlling traits such as shattering (qSH1, sh4), erect growth (PROG1) or unpigmented seeds (Rc), all suggested a single origin for all cultivated rice (Konishi et al. 2006; Lin et al. 2007; Sweeney et al. 2007; Tan et al. 2008; Zhang et al. 2009). This conclusion was also supported by multi-locus phylogenies based on diverse markers, including nuclear gene sequences (Molina et al. 2011), RFLPs (Restriction Fragment Length Polymorphisms: Lu et al. 2002), microsatellites (Gao & Innan 2008) and whole-genome sequencing of 1083 indica and japonica cultivated rice varieties and 446 O. rufipogon accessions from all over Asia (Huang et al. 2012). In contrast, other phylogenetic studies concluded that indica and japonica (as well as other varieties) were independently domesticated in different regions, including China, India or Thailand. These comprise analyses on nuclear RFLPs (Wang et al. 1992), four nuclear genes (Zhu & Ge 2005), a haplotype network of both nuclear and chloroplast sequences (Londo et al. 2006), DNA sequences from 22 nuclear loci (Rakshit et al. 2007), whole nuclear genomes (Yang et al. 2011) or whole-chloroplast sequences (Civáň & Brown 2016).
Even the whole genome dataset published by Huang et al. (2012) has been re-analysed in a way that shows three independent domestimations of rice (Choi et al. 2017; Civán et al. 2015; but see also Huang & Han 2015).

The contrasting results in rice arise from the combined choices of phylogenetic methods, markers and sampled accessions, rather than any one of these factors in isolation. Efforts have been made to reconcile both claims considering de novo domestications that replaced independently domesticated local varieties (Sang & Ge 2007), extensive introgression and selection (He et al. 2011), the roles of past demographic processes in both rice and wild rice populations (Choi et al. 2017), the influence of population structure in phylogenetic inference (Kim et al. 2016) and the confusing effect of feral and weedy varieties mimicking wild plants (Qiu et al. 2017; Wang et al. 2017). We return to this question below.

Archaeobotanical data and their interrelation with phylogenetic inference: fast versus protracted domestication scenarios

The speed of domestication (that is, the rate of fixation of phenotypic traits) has emerged as a major theme from the controversies and complex answers associated with questions of single versus multiple domestimations. This in turn has led to debate over which traits were selected in the primary domestication episode and which represent crop improvement post-domestication, for example selection for waxy maize starch (Fan et al. 2009) or loss of photoperiod sensitivity (H. Jones et al. 2008). The former traits show a clear phenotypic dimorphism between the wild progenitor and the domesticate (Abbo et al. 2014). They result from mutations in a few loci, with major effects, whose resulting phenotypes would have been visible in populations, positively selected by early farmers, and hence fixed in ancient crop populations (Lin et al. 2012). The latter have accumulated over millennia of crop evolution, and often show a phenotypic continuum. These include alterations in flowering-time pathways, increased seed size, pest and disease resistance, grain quality and the loss of appendages that aid seed dispersal, such as awns. A key issue here is how many genes and mutations were required for a critical domestication transition of wild to domesticated (Sang 2009). Spike brittleness is the trait most strongly associated with domestication for the annual cereal crops, and sometimes considered to be the only trait that reliably distinguishes between wild and cultivated forms, for example in barley (Hordeum vulgare subsp. spontaneum and H. vulgare subsp. vulgare, respectively; Pankin & von Korff 2017). The evolution of other traits, specifically the naked caryopsis and six-rowed spike characters in barley, are also major domestication traits, but appeared over a millennium later than the tough rachis and the global domesticated barley genepool remains polymorphic for these two traits today (Sang 2009).

Early theoretical and field work suggested that domestication trait alleles, such as those controlling rachis fragility, can become fixed in wild plant populations in a few generations given intense human selection for desired traits (Hillman & Davies 1992). Yet for these to be fixed in a population, reproductive isolation from plants carrying the wild alleles was necessary, and this process would have taken a long time (protracted model). Martin Jones and Terry Brown (2007) argued that reproductive isolation was at least as important, or more important than, strong selection in driving the transition to ‘full domestication’, in the sense of populations showing a high frequency of the human-selected phenotype.

Protracted domestication scenarios may explain why phylogenetic interpretations are not always corroborated by archaeological data. Martin Jones and colleagues questioned the interpretation of Heun and colleague’s (1997) genetic analysis of einkorn, which localized its domestication in the Karaca Dağ mountains. The oldest archaeobotanical remains with signs of domestication (plumper kernels and rough rachis-breakage scars) do not come from sites in this region, but from the southern Levant (Brown et al. 2009; Fuller et al. 2011; M. Jones et al. 1998). In the case of emmer wheat, the earliest archaeobotanical remains with a rough breakage scar (indicative of a tough rachis, considered by some authors the only definitive domestication trait), come from northern sites of Cayönü and Cafer Höyük (8250–7550 cal bc), not far from where genetic data indicated its single origin (Zohary et al. 2012). Some archaeobotanists, however, consider that the observed increase in size and changing shape of grains is also diagnostic of domestication (Brown et al. 2009). This would imply that a mixture of domesticated and wild emmer was cultivated together for millennia during the Pre-Pottery Neolithic B (PPNB) in southern Levant sites such as Tell Aswad and Jericho (Feldman & Kislev 2007). According to this school of thought, the fixation of the tough rachis trait took place later and does not in itself define domestication. Other authors consider that increased grain size may represent pre-domestication cultivation; this may largely reflect differing definitions of domestication.

The archaeobotanical record of wheat and barley in the Near East, and rice in China, shows wild and domesticated forms, defined by rachis scars or grain size, occurring in variable proportions for
almost 4000 years until domesticated forms become exclusive (Fuller et al. 2014). Likewise, the presence of arable weeds associated with wild plant remains in the archaeological record suggests that intensive cultivation of wild species preceded full domestication in both the Near East and China (Arranz-Otaegui et al. 2016; Weiss et al. 2006; Willcox & Stordeur 2012). Similar patterns have been proposed for some non-cereal species, for example lentil (Lens culinaris ssp. culinaris: Abbo et al. 2009; Sonnante et al. 2009).

The body of emerging evidence for a protracted transition to morphologically domesticated forms highlights that the paradigm of discrete ‘domestication events’ found in some of the phylogenetic literature is, at best, an oversimplification and, in some cases, seriously misleading. While the fixation of a domestication trait allele may take millennia and occur over a wide geographical area, the initial mutation that gives rise to that allele has a defined point in space and time, and can be characterized at the DNA sequence level.

Inferences from domestication ‘switch’ genes

The growth of functional genomics approaches from the mid 2000s facilitated the discovery of genes underlying these key crop domestication traits (Olsen & Wendel 2013; Ross-Ibarra et al. 2007). This has enabled direct analysis of the number of evolutionary switches leading to the domesticated phenotype. Work has focused mostly on the rachis phenotype of cereals, which is typically under the control of one or a few loci with major effects. In einkorn wheat, a single mutation is responsible for the non-brittle rachis, leading to the inference of a single domestication event that equates to the fixation of this allele in the cultivated population (Zohary 1999). By contrast, in barley there are three independent mutations, each of which confers the tough rachis phenotype, two in the brittle rachis Btr1 gene and one in Btr2 (Azhaguvel & Komatsuda 2007; Civán & Brown 2017; Pourkheirandish et al. 2015). The two mutations described by Azhaguvel and Komatsuda (2007) have differential distributions in the east and west Fertile Crescent. These are associated with distinct domesticated lineages, leading to the long-established separation of ‘occidental’ and ‘oriental’ types of barley (Takahashi 1955), which is backed up by other genetic studies (Morrell & Clegg 2007; Morrell et al. 2013; Saisho & Purugganan 2007). In sorghum, there are three non-shattering haplotypes at the Shattering1 (Sh1) locus; from the distributions of these non-shattering haplotypes among sorghum landraces, it is suggested that three geographically separated human populations independently selected for the non-shattering phenotype (Lin et al. 2012). These studies provide appealingly clear answers, but the challenge is to relate the evolutionary trajectory of loci with a major effect on domestication traits, particularly grain shattering, to those of loci controlling grain size and shape, where multiple loci and the environment each contribute modestly to the phenotype.

Towards an accommodation of on-going wild-domestic gene flow

The paradigm of protracted domestication allows for continued gene flow between individuals with domesticated alleles and their wild counterparts. On-going introgression is likely where a domesticated plant population is in sympathy with the wild population; a large proportion of plant crop species maintain gene flow at least in some part of their range (Ellstrand et al. 1999; Jarvis & Hodgkin 1999). The consequence of on-going gene flow is that phylogenetic methods appropriate for reconstructing macroevolutionary lineages of species across different genera, families or phyla evolving through vast spans of time may not always be suitable for analysing closely related taxa that are in the process of diverging or have done so only in the past few millennia, as is the case with crops and their wild progenitors. Results are thus confounded by the biological realities of hybridization, ferality, selection, recombination and the mode of reproduction. To detect these processes, both statistical refinements of phylogenetic methods which explicitly model gene flow and alternative clustering methods, which make different assumptions about the evolutionary process, are employed. Canonical clustering methods (e.g. Principal Components Analysis, PCA) represent genetic similarity and differentiation in a way that makes few assumptions about the evolutionary process. Bayesian- and likelihood-framework clustering methods, as implemented in the widely used software STRUCTURE (Pritchard et al. 2000), ADMIXTURE (Alexander et al. 2009) and others, enable probabilistic inference of distinct populations, assigning individuals to populations, analysing hybrid zones, identifying admixture and migrants and estimating population allele frequencies. The domestication history of a crop is recorded in patterns of genetic diversity within and between individuals and populations and in its relationship to wild progenitors (Fig. 15.2).

Since the early 2000s, such methods have been a standard part of the toolkit for inference of domesticated origins, enabling comparative evaluation of distinct geographical hypotheses. Occasionally, such methods have resolved apparently straightforward scenarios. Identification of genetic clusters in wild and
domesticated populations of sunflower (*Helianthus annuus*) supported a single origin of domesticated sunflower in eastern North America (ENA; Blackman et al. 2011). Wild *H. annuus* from Mexico and ENA divided into two genetic groups based on geography, while domesticated varieties from both regions showed a very high proportional allocation to the ENA gene pool, with very low levels of genetic input from the wild Mexican cluster.

In contrast, in the case of another major New World domesticate, maize (*Zea mays*), the phylogenetic inference of a single origin from the lowland Mexican ancestor Balsas teosinte (*Zea mays* subsp. *parviglumis*: Matsuoka et al. 2002) was substantially refined by the
use of non-phylogenetic approaches. The most ancestral domesticated lineages were found in highland Mexico, which was puzzling, given the lowland distribution of Balsas teosinte. This ‘ecological paradox’ was resolved by analysis of a SNP dataset using PCA and Bayesian clustering approaches. Results demonstrated that a different teosinte (Zea mays subsp. mexicana) had been hybridizing with highland domesticated maize, rendering this maize population genetically similar to Z. mays subsp. parviglumis. Subsequent analyses inferred the location of domestication in the Mesoamerican lowlands, congruent with archaeological, ecological and biogeographical evidence (van Heerwaarden et al. 2011).

Prior to the next-generation sequencing revolution, the optimal domesticate-wild relative system for studying introgression was one where gene flow occurred at moderate levels (Jarvis & Hodgkin 1999). With the advance in high-throughput methods, introgression in both frequently hybridizing, out-crossing crop species like maize and inbreeding species that hybridize with low frequency can be achieved in high resolution. The trajectory of research on barley illustrates how advances in genomics technologies have altered both the nature of the questions asked and the way we address them, in little more than a decade. A Bayesian clustering study based on DNA markers sparsely distributed through the genome found two genetic clusters in both wild and domesticated barley, leading to the inference of two geographically separated domestications (Morrell & Clegg 2007). Recent genome-wide analyses using dense coverage across all chromosomes have revealed complex patterns of genetic ancestry. Poets and colleagues (2015) showed that cultivated barley has a mosaic ancestry with wild populations across its range contributing differentially to the genome of domesticated barley in the Near East. While a tough rachis mutant must come from a specific locality, the geographic origin of the overall genomes in a domesticated population should not be attributed to the same location. Introgression events may date back to the early history of widespread barley cultivation, as linkage blocks were not shared between cultivated and wild populations (Fig. 15.2). These patterns may well hold true for other crops, such as emmer and einkorn (Allaby 2015).

Phylogenetic methods whose assumptions are particularly suited to closely related samples, including phylogenetic networks, and statistics applied to phylogenetic trees, have been developed to allow and test explicitly for gene flow between wild and domesticated plants (Mardulyn 2012). Phylogenetic networks applied to DNA sequences from 18 loci supported the hypothesis of a single domestication of einkorn in Turkey (Kilian et al. 2007). For emmer, however, these methods revealed contributions from different wild populations to domesticated ones, supporting multiple domestications (Civáň et al. 2013). Some authors have proposed models that account for the inconsistencies in the emmer wheat results, such as a pre-domestication stage of cultivation and movement of wild wheat (Fuller & Colledge 2008), or the dispersed-specific model (Kilian et al. 2010). Another possibility is that some accessions classified as wild are in fact feral varieties descending from domesticated individuals which escaped cultivation and, either by selective pressures or by hybridization with wild plants, have acquired a wild phenotype (Oliveira et al. unpublished data).

As illustrated in the case of maize discussed above, on-going introgression into a domesticated crop may involve more than one related wild species or subspecies, rather than just one wild ancestral taxon. Phylogenomic methods can be harnessed to trace the history of emergence of a domesticated lineage, and subsequently allele frequency statistics can be applied to that phylogenetic framework to test for past introgression. The recently developed D statistic, commonly applied as the ABBA-BABA test (Green et al. 2010), detects asymmetry in three-population gene trees. The premise is that gene flow between closely related populations causes this asymmetry. A strength of this method is that it can detect archaic admixture even in the absence of archaic samples. In analysis of common bean (Phaseolus vulgaris; Rendón-Anaya et al. 2017), alleles underlying domestication traits characteristic of common bean originated from several local wild populations, revealing signatures of adaptive introgression from local populations of diverse wild species. These analyses depend upon meaningful delimitation and identification of sampled taxa and populations, which is not always straightforward in practice.

A modified version of the ABBA-BABA test, the $D_{FORK}$ test (Pease & Hahn 2015), can handle phylogenies with more taxa and reliably detects introgression and its direction, even if present at low levels. This method, combined with coalescence-based modelling, has recently been applied to rice (Choi et al. 2017). Results validate the ‘multiple origin, single domestication hypothesis’. This proposes that Oryza sativa ssp. indica and ssp. japonica had phylogenetically distinct origins, but the origin of domestication traits was unique to ssp. japonica. These traits were subsequently ‘captured’ by introgression into ssp. indica and ssp. aus. The model suggests a resolution of the heated debate about the number of rice domestications, highlighting the distinct processes of crop phylogenetic origins and
domestication trait acquisition. Choi and colleagues comment ‘in the end, our analysis calls into question how we conceptualize our definition of domestication’, supporting our dissection of ‘origins versus domestication’ above.

Conclusion

Evolutionary transitions from wild to domesticated crop forms, driven by the selective pressures imposed by human manipulation of plant life cycles, are beguiling as plausibly discrete events that took place in narrowly circumscribed tempo-spatial locations. This notion is reinforced by the legacy of Vavilov’s ‘centres of origin’ concept, even though Vavilov’s centres were geographically broad and many aspects of the evolutionary process were beyond the scientific currency of his time. A framework of domestication ‘events’ maps neatly onto the apparently unambiguous ‘centres of origin’ concept, even though Vavilov’s centres were geographically broad and many aspects of the evolutionary process were beyond the scientific currency of his time. A framework of domestication ‘events’ maps neatly onto the apparently unambiguous topology of phylogenetic trees, which have dominated much research on crop origins. The ‘single or multiple domestications’ question relates naturally to this macroevolutionary model. In the last decade, however, complementary insights from archaeobotanical and genomic data show that the picture is rarely that black-and-white, and that the microevolutionary processes of population genetics give rise to a geographically far more complex interrelation between forms designated ‘wild’ and ‘domesticated’. Nevertheless, the quest for geographic patterns in the evolution of crop genomes remains intensely worthwhile. The challenge in the interdisciplinary dialogue between archaeologists, archaeobotanists and plant and evolutionary biologists, with their different emphases on the human, plant morphological and genomic shifts, is to re-explore the meaning of ‘domestication’ in a common language, retaining this umbrella term where it is useful, but also advancing explicit mutual understanding of the underlying processes.

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