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Ancient Plant DNA as a Window Into the Cultural Heritage and Biodiversity of Our Food System

Natalia A. S. Przelomska[1,2]*, Chelsey G. Armstrong[3] and Logan Kistler[1]*

[1] *Department of Anthropology, Smithsonian Institution, National Museum of Natural History, Washington, DC, United States,*
[2] *Comparative Plant and Fungal Biology, Royal Botanic Gardens, Kew, Richmond, United Kingdom,* [3] *Department of Anthropology, University of British Columbia, Vancouver, BC, Canada*

Since the beginning of the ancient DNA revolution in the 1980s, archeological plant remains and herbarium specimens have been analyzed with molecular techniques to probe the evolutionary interface of plants and humans. In tandem with archeobotany, ethnobiology, and other methods, ancient DNA offers tremendous insights into the co-evolution of people and plants, and the modern genomic era offers increasingly nuanced perspectives on plant use through time. Meanwhile, our global food system faces threats linked with declining biodiversity, an uncertain climate future, and vulnerable crop–wild relatives. Ancient plant DNA does not yield easy answers to these complex challenges, but we discuss how it can play an important role in ongoing conversations about resilience, sustainability, and sovereignty in our food system.

Keywords: archaeogenomics, ethnobiology, agrobiodiversity, food security, domestication, archaeobotany

INTRODUCTION

Vascular plants are foundational to all terrestrial ecosystems, and have been around for hundreds of millions of years. The flowering plants—Angiospermae, the largest and most diverse group in the plant kingdom—arose ∼140–250 million years ago (Magallón et al., 2015; Foster et al., 2017), and over this time they have evolved an astounding range of diversity in functional and developmental traits, genome characteristics, and physiology across almost 300,000 known species (Christenhusz and Byng, 2016). The genus *Homo* began to co-habit with plants a mere ∼2.8 million years ago (Hublin, 2015) and a multitude of co-evolutionary relationships between plants and people ensued (Nabhan, 2002; Allaby et al., 2015).

The co-evolution of plants and humans is most prominently exemplified by the emergence of domesticated plants during the Holocene—the epoch beginning around 12,000 years ago after the last ice age—leading to the evolution of agricultural ecosystems and economies, and resulting in massive societal and ecological shifts. Wild plants and their domesticated counterparts thrived in sympatry and continued to interbreed over the course of a protracted domestication process (Purugganan and Fuller, 2011; Allaby et al., 2017). A vast number of other plant species are valuable to humans, but have not been subjected to evolutionary pressures resulting in domestication. The proportion of the world's botanical biodiversity with known uses by humans is estimated to include around 10%, or ∼31,000 species. Of these, 57% are medicinal, 36.5% used for materials and clothing, and 17.8% for food (Royal Botanic Gardens Kew, 2016).

Our current food systems have been profoundly shaped by changes to agriculture that took place after the industrialization of farming methods—breeding for more efficient cultivation, high, uniform yield, large-scale mechanization, and trends toward monocultures. Modern crop practices

can therefore overshadow much of the ecological innovation that came before, largely in the hands of Indigenous cultivators. Significant knowledge pertaining to the past usage of plants persists in historical-ecological records, and in traditional knowledge systems and practices. Garnett et al. (2018) estimate that at least 28% of the world's land surface is owned/managed by Indigenous peoples, including some of the most biologically diverse ecosystems on Earth. In some cases these ecosystems include managed perennials and cultivars that have been maintained for millennia (Chouin, 2009; Turner, 2014; Clement et al., 2015; Ford and Nigh, 2016).

The application of archeological science has been hugely successful for complementing traditional knowledge and exploring deeper-time evolutionary and cultural processes surrounding domestication (e.g., Hoffmann et al., 2016). Archeobotany has been valuable for determining the chronology and composition of past agroecosystems (Bakels and Jacomet, 2003; Smith and Yarnell, 2009; Motuzaite-Matuzeviciute et al., 2013; d'Alpoim Guedes et al., 2014), studying the domestication syndrome (Nesbitt, 1998; Fuller et al., 2019), and elucidating past diets with significant time-depth—for example demonstrating a long-term reliance of early humans on starchy foods (Larbey et al., 2019).

At the same time, we live in a moment when the security of our food systems is a subject of global concern (Tscharntke et al., 2012). The most critical conversations for food security and food sovereignty, sustainability, and ecological impact should revolve around land and energy use, agricultural practices, biodiversity priorities, and the threat of worsening global climate uncertainty for predictable growth seasons and crop yields. However, looking to the past 10,000 years of crop evolution and plant use offers context, and could thus contribute to developing solutions, for these important issues.

ANCIENT DNA: UNRAVELING PATHWAYS TO DOMESTICATION

In combination with archeobotany and other anthropological and analytical methods, ancient DNA (aDNA) is a particularly exciting means for opening doors to the human past using plant remains (Gutaker and Burbano, 2017; Allaby et al., 2018; di Donato et al., 2018; Pont et al., 2019). Ancient plant genomics allows us to address increasingly nuanced questions regarding plant cultivation and domestication, such as the relationships between crops and wild relatives, routes of plant dispersal mediated by humans, and plant traits whose evolution was instrumental to domestication. For example, we are now able to examine shifting allelic makeup for traits related to domestication (e.g., Mascher et al., 2016; Ramos-Madrigal et al., 2016), probe the adaptive trajectories of plants carried into new environments (e.g., da Fonseca et al., 2015; Swarts et al., 2017), infer culinary and other crop-linked cultural preferences (e.g., Castillo et al., 2016), gain insights regarding the source of genetic variants under selection (novel mutations, standing variation, or introgression; Gutaker et al., 2019a), and estimate the extent and timing of admixture with wild relatives

and introduced lineages (Mascher et al., 2016; Scott et al., 2019).

The majority of archeobotanical remains are preserved by charring, but unfortunately this process does not preserve ancient DNA at predictable or useful levels for genomic analysis (Nisterlberger et al., 2016). Similar to most subfields of trace sciences (archeology, paleoecology), archeobotanical contexts boasting the outstanding preservation necessary for aDNA analysis over extended archeological time are typically restricted to dry caves or rockshelters, extremely arid localities, or waterlogged deposits. Maize has been particularly productive due to its widespread importance throughout the pre-colonial Americas, and maize remains suitably preserved for genomic analysis have been found in Mexico, the southwestern US and Colorado Plateau, the Andes, and caves in lowland Brazil (da Fonseca et al., 2015; Ramos-Madrigal et al., 2016; Vallebueno-Estrada et al., 2016; Swarts et al., 2017; Kistler et al., 2018).

Application of a target sequence capture approach on 32 maize samples spanning 5,910 to 670 years old in Mesoamerica and the Southwest illuminated routes of maize dispersal into the United States, and the timing of selection on genes associated with adaptation to the challenging new environment (da Fonseca et al., 2015). Further aDNA research revealed that maize adapting to these new environments could be only marginally suited to the unfamiliar growth conditions (Swarts et al., 2017), highlighted a long-lasting, intertwined relationship between maize and its wild progenitor *Zea mays* ssp. *parviglumis* (Ramos-Madrigal et al., 2016; Vallebueno-Estrada et al., 2016), and indicated that the cultivated gene pool was subdivided and carried away from the domestication center before domesticated forms were robust and stable (Kistler et al., 2018). Combining these insights with previous work highlighting the role of adaptive crop–wild gene flow in maize evolution (van Heerwaarden et al., 2011), and the long-term decay of genetic diversity in maize (Wang et al., 2017), aDNA fills in critical elements of the complex, protracted evolutionary process leading to the world's most abundant grain crop (Food and Agriculture Organization of the United Nations, 2018).

Another fortuitous archeobotanical time series presented itself in sorghum remains (*Sorghum bicolor*), preserved in the fortified hilltop city of Qasr Ibrim in the Lower Nubian Desert—present-day Egypt (Smith et al., 2019). Sorghum seeds spanning 1,805 to 450 years old were used along with herbarium and modern specimens to dissect genetic diversity and human selection over time. Additionally, this study showed a long-term loss of genetic diversity through archeological time up to the present day, highlighting the continuous erosion of biodiversity under human influences.

In other species, archeogenomics has provided fundamental insight regarding the evolutionary ecology and long-term niche of domesticates (squashes; Kistler et al., 2015), shifting baselines of genetic diversity through time (sunflowers; Wales et al., 2019), genomic structural upheaval since domestication (cotton; Palmer et al., 2012), and extreme kinship networks and clonal lineages spanning millennia (grapevine; Ramos-Madrigal et al., 2019). In emmer wheat, a species with a particularly large and complex genome, the recently reported genome

from a 3,000-year-old specimen revealed significant tracts of diversity absent from modern wheats, underscoring the loss of crop genetic variation over time (Scott et al., 2019). These examples rely on ancient genomics to help build the conceptual foundation of domestication science, which serves as important background to help inform the future of agroecosystems resilience globally.

The genetic basis of local adaptation to new habitats is a subject particularly suited to ancient and historic plant DNA. Throughout their history, crop plants have been routinely presented with novel growth conditions when moved into new habitats by humans. These comprise changes in daylength and temperature, UV exposure, soil conditions, symbiont availability, and other abiotic and biotic variables. The amenability of a staple crop to grow in new regions was critical to the mobility of early farming communities, and many of the same adaptive strategies could be of interest in the present day given our changing climate and conditions of land-use. The mechanisms underpinning these adaptations is therefore of interest to both domestication scientists and contemporary crop breeders.

One such adaptation that can unlock a range of new agroecological niches is the loss of sensitivity to photoperiod (daylength), which in many plants determines time of flowering. Selection pressure on responsiveness to photoperiod has been important in influencing the rate of post-domestication range expansion in many crops (Purugganan and Fuller, 2009), for example permitting the northward spread of rice, barley, beet, and flax from their native ranges (Fujino and Sekiguchi, 2005; Lister et al., 2009; Pin et al., 2012; Gómez-Ariza et al., 2015; Gutaker et al., 2019b). These studies draw on the gene pool available in either landrace or cultivar germplasm material, but even more detailed information can be retrieved using samples that provide time depth. For example, using data from 1,900-years-old maize cobs from Colorado and a modern germplasm panel for comparison, Swarts et al. (2017) demonstrated that alleles associated with early flowering had already been selected for from the extensive standing variation, as an early step in adaptation to more temperate latitudes.

In the absence of archeological samples—the prevailing situation for root crops—herbarium specimens are excellent repositories of valuable genomic information along similar lines at shallower time-depths. For example, Gutaker et al. (2019a) demonstrated with historical genomes from herbaria that long-day adaptation of European potato lineages was most likely due to *de novo* variants arising in their genomes after their arrival in Europe. Furthermore, that study showed that the early European potato genomes were already pre-adapted to this daylength response due to modifications in the gibberellin pathway—a hormonal signaling system mediating tuber bolting time in response to daylength—which occurred prior to their trans-Atlantic dispersal. There has been a recent surge in the use and function of herbarium collections, most notably in conservation biology (Krupnick et al., 2009). However, there has been little inclusion of cultural knowledge, societal values, or domestication history associated with specimens upon their collection. This is surprising given that many of the first herbaria were deeply motivated by ethnobotanical questions (Martín et al.,

2010). The early call for collectors to be more mindful of the genetic preservation of specimens (e.g., storing tissues with silica gel), is followed up by another call to curate ethnobotanical and cultural knowledge with specimens in order to better situate collections for research relating to food security/sovereignty, agroecology, and biocultural diversity (Stepp and Thomas, 2007; Nesbitt, 2014).

Past plant–human interactions are best understood when a multidisciplinary approach is applied (e.g., Dalby, 2013), and ancient genomes can be a powerful means to complement or verify historical records. Paris (2015, 2016) summarized how discovery of 4,000-years-old seeds of watermelon (*Citrullus lanatus*) in conjunction with biblical records and iconography, as well as linguistics, can shed light on the cultivation history of this cucurbit crop. A recent study built upon these insights by investigating a 3,500-years-old *Citrullus lanatus* leaf from a Pharaonic tomb using genomic methods, further illuminating the origins of watermelon by revealing that New Kingdom Egyptians were already consuming a pink-fleshed and sweet variety (Renner et al., 2019).

PLANT BIODIVERSITY AND FOOD SECURITY

One important consideration for agricultural sustainability is population genetic health of crops over time, manifested as both erosion of genetic variation and the accumulation of harmful variants. Current threats to the Cavendish banana—the top commercial banana variety comprising 99% of the global export market—illustrate an extreme case of the risk in lost diversity. Plantations of Cavendish are succumbing to *Fusarium* wilt tropical 4 (TR4), resulting in massive worldwide losses (Solly, 2019). Cavendish is favored because of its storability and stability in shipping, but as a result, the entire export banana market relies on this single cultivar lacking resistance to the current pathogenic threat. This fungal pathogen reached the Americas just last year, and now threatens all the world's key banana-producing regions (Galvis, 2019; Solly, 2019).

A similar scenario created conditions for the Great Famine in nineteenth century Ireland, killing over a million and displacing the same number again (Turner, 2005). Several strains of potato were grown by vegetative propagation in Europe at the time, but their diversity was a subset of their South American landraces of origin, and they had been shaped by adaptive stressors of the new growing environment (Gutaker et al., 2019a). A pathogenic oomycyte, *Phytophthora infestans*, caused years of devastating crop losses since these potato varieties lacked resistance in the population (Austin Bourke, 1964; Saville et al., 2016). DNA from herbarium specimens revealed that it was likely a resurgence of older, blight-resistant landraces with higher proportions of Andean ancestry that re-invigorated European potato production (Gutaker et al., 2019a). These are extreme examples where vegetative propagation facilitates particularly low field-level diversity, but they highlight the vulnerabilities of low diversity and a lack of genetic resilience to such pathogenic onslaughts.

Another consideration for food system resilience is the accumulation of deleterious genetic mutants due to the demographic strain of agriculture on crops. In many other crop (and domestic animal) species analyzed so far, this "mutation load" has increased significantly in domesticated lineages compared with wild forms (Liu et al., 2017; Wang et al., 2017; Smith et al., 2019), with ultimate fitness effects threatening cultivated populations (Kono et al., 2016; Kremling et al., 2018). Recent studies in both plants and animals highlight that the mutation load, though linked with long-term dispersal (Kistler et al., 2018) and demography (Wang et al., 2017), has in some species spiked in recent centuries (Gaunitz et al., 2018; Kistler et al., 2018). Therefore, much of the elevated modern-day mutation load may be the result of recent breeding activities as opposed to the protracted emergence and long-term traditional curation of domesticated species.

Cassava (also called manioc or yuca) is the world's sixth leading food plant, feeding 800 million as a staple crop and cultivated across a pan-tropical range with an Amazonian origin (Food and Agriculture Organization of the United Nations, 2013, 2014). However, genomic analysis reveals that it suffers an excess of deleterious genetic variants—a high mutation load (Ramu et al., 2017). Cassava is propagated almost exclusively by vegetative stem cuttings, while its wild counterpart reproduces by out-crossing. Therefore, researchers have hypothesized that this shift toward clonal propagation since domestication has pre-empted the wild plant's abilities to purge its genome of harmful variants through recombination (Ramu et al., 2017). Thus, by bringing the plant into cultivation and altering its reproductive biology, humans have created an important food source with the unintended consequence of introducing genomic vulnerability.

The case of sorghum presents a contrasting view of the mutation load in crops. Sorghum, the world's most important cereal crop in arid regions, is widely grown as a staple food particularly in developing nations in Asia and Africa (Food and Agriculture Organization of the United Nations International Crops Research Institute for the Semi-Arid Tropics, 1996). Like other domestic species, the mutation load is elevated compared to the wild progenitor. However, archeogenomic time-series analysis from Qasr Ibrim in modern-day Egypt revealed that ancient farmers took advantage of periodic hybridization between lineages to boost diversity and ameliorate the mutation load in real time (Smith et al., 2019). Thus, in some species, traditional management strategies have pre-empted this burdensome accumulation of harmful variants.

Some researchers call for protecting the biodiversity of our food systems at higher levels of organization, namely by prioritizing species and ecosystem biodiversity in our food production pipeline (Hammer et al., 2003; Wood et al., 2015), and this is thought to be most feasible through deployment of diverse local domesticates (Shelef et al., 2017). A vast proportion of human nutrition globally (>90% calories) is derived from just 20 plant species (Massawe et al., 2016), where the dominance of rice, wheat, and maize was facilitated by the Green Revolution commencing in the 1960s. This agricultural transition brought immediate public health and ecological benefits in some regions, including short-term reduction of poverty and temporary reduced deforestation through higher crop yields. The Revolution, however, exposed asymmetries of power dynamics in cache crop economies (Shiva, 1992), and revealed a global Achilles heel in crop field resilience: The global reliance on such a low diversity of plant species can result in higher risks of large-scale famine.

Climatic predictions for the near future raise another set of concerns for crop sustainability (Khoury et al., 2014). Rice, for example, is particularly vulnerable to climate change, where both flooding and drought stress can cause complete crop failure (Nguyen, 2005). However, wild rice (*Zizania palustris*) is highly adaptive to these specific features of climate change and, coupled with Indigenous Anishinaabeg knowledge (e.g., harvest protocols, life histories, grain quality) has the potential to enlighten breeding programs aimed specifically at climate change resiliency (Zilberstein, 2015). Increasing the species diversity and genetic diversity of agricultural systems improves the resilience of our food systems, and may often be best implemented at local scales (Mijatović et al., 2013). Local distribution centers are a key factor in this effort, for example supporting diversity of apple varieties in the US (Goland and Bauer, 2004).

The traditional knowledge of Indigenous famers is a key component of a diversified approach for ensuring that agricultural landscapes thrive into the climatically unstable future (Makondo and Thomas, 2018). As an example, traditional knowledge used for managing yam (*Dioscorea* spp.) crops in Oceania has led to the emergence of valuable hybrids—confirmed by a phylogenetic analysis using herbarium specimens—whose existence could be relevant to the future management of this staple crop (Chaïr et al., 2016). The diversity in traditional landraces is also greater than in breeding programs and industrialized cropping contexts. For example, molecular analysis revealed that diversity sampled from an *ex situ* cassava core collection was matched by indigenous landraces from a single village in Guyana (Elias et al., 2000). Indigenous peoples who have occupied the same landscape for centuries or indeed millennia have had to, unavoidably, manage their food resources through extensive oscillations in weather, climate, and general environmental change. As a result, the codified knowledge of what, and how, to plant is extensive, and the diversity of germplasm maintained is extraordinary (Anderson, 2016).

Studies involving ancient DNA and archeobotanical remains alongside ethnobotanical knowledge may inform and encourage cultivation of valuable plant species which have been marginalized in recent times. For instance, beaked hazelnut (*Corylus cornauta*) in the Pacific Northwest is perceived as an obscure crop in management terms, but surveys of traditional knowledge expose its deep cultural significance, with uses as food, medicine, and construction material (Armstrong et al., 2018). Recently, this species has also been used in hybridization programs given its resistance to Eastern filbert blight (caused by *Anisogramma anomala*), which has been globally devastating for European hazelnut (*Corylus avellana*) crops (Muehlbauer et al., 2014; Oregon State University., 2019). In northeastern North America a whole complex of plants lost for generations and only known as cultigens from archeobotanical evidence include knotweed (*Polygonum erectum*), sumpweed (*Iva annua*), and

chenopods (*Chenopodium berlandieri*) of eastern North America (Mueller et al., 2017). These species are good candidates for potential re-domestication, which could simultaneously work against low food biodiversity and economic insecurity in rural North America (Mueller et al., 2017).

Similar marginalized crops elsewhere include the Bambara groundnut (*Vigna subterranea*) native to Africa, and finger millet (*Eleusine coracana*) grown in arid areas of the Indian subcontinent and Africa. Both have been historically dubbed a "poor man's crop" (Azam-Ali et al., 2001; Joshi and Joshi, 2002), but are robust in environments prone to drought, and are nutritionally valuable. Similarly, the Asian millets foxtail (*Setaria italica*) and broomcorn (*Panicum miliaceum*) were not popular enough to become a staple food crop in the past (Lightfoot et al., 2013), but early domestication, flexible seasonality, and persistence seen in the archeological record meant that these hardy crops played a crucial role in facilitating humans' mobility (Jones et al., 2016). The role of multidisciplinary research with an ancient DNA element concerning these marginalized species is much more than strictly scientifically and economically applicable—it highlights the importance of maintaining food sovereignty and preservation of cultural heritage (Coté, 2016).

CONCLUSIONS

Theories emerging from plant archeogenomics can contribute in a significant way to the understanding of the evolution of plants and plant genomes; domestication serves as an excellent model system for evolution (Piperno, 2017; Zeder, 2017). Contemporary domestication paradigms stemming from this work highlight key concepts that could be instrumental to decision-making with regard to future food systems. However, complementary research on lesser known crops, other plant species that are valuable to humans, and the community ecology of these species is still lacking (see Deur and Turner, 2005). A much more direct application of ancient genomes for the enhancement of our food systems could be mining for useful past traits lost in modern crop fields, but potentially recoverable through crop–wild relatives.

The unstable condition of our food systems is, in part, a biodiversity problem. Several strategies have been put forward to alleviate the burden of scant biological diversity at the highest production levels in our food systems (Tscharntke et al., 2012). One is the improvement of the diversity of elite crops, which can be introducing new traits through breeding or genetic modification. Gene editing using CRISPR-Cas9 technology has in fact been successfully used to produce pathogen-resistant bananas (Tripathi et al., 2019), but these face regulatory obstacles and offer no guarantee of resistance into the future (Maxmen, 2019).

Other approaches involve drawing on diversity already available, which is introduced either through crossing of wild relatives with cultivated varieties or utilizing the wild relatives themselves. Such a "substitution-diversification" strategy could promote species better suited to future climates and push more plant species down the spectrum of domestication (Borrell et al., 2020). Both dimensions of this approach highlight that extensive diversity, which has emerged due to evolutionary pressures over millennial timescales, can be harnessed to its fullest potential, rather than endangered due to an increased reliance on genetically homogenous cultivars (Bevan et al., 2017).

Twenty percent of described angiosperms are threatened with extinction (Brummitt et al., 2015), and the IUCN has recently recognized the attendant risks to food production by recognizing a wide range of crop–wild relatives threatened by habitat disturbance (Maxted and Dulloo, 2017). Ancient plant genomics is not the solution to our food biodiversity predicament. However, it can provide nuanced, long-term insight into where we are and how we got here with respect to the evolution of the species that feed the world.

DATA AVAILABILITY STATEMENT

All datasets analyzed for this study are included in the article and the supplementary files.

AUTHOR CONTRIBUTIONS

NP and LK drafted the manuscript. All authors contributed the text, revised, read, and approved the submitted version.

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