PNAS NEWS FEATURE

Unearthing the origins of agriculture

Archaeobiology is offering new insights into the long-debated roots and evolution of the practice that made large human settlements and our modern complex society possible—even if at a cost.

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Big Agriculture has its roots in the advent of human farming activities that started nearly 12,000 years ago, an origin story that archaeobiologists and other researchers are still trying to parse. Image credit: Science Source/Stockr.

As the last great ice sheets were retreating and the Pleistocene Epoch was ending, humanity began an epic journey. For hundreds of thousands of years, our ancestors had survived by hunting animals and gathering edible wild plants. But starting about 11,700 years ago, people began to use wild plants in ways that changed the plants themselves, a process called domestication. People also began to alter their environments as they cultivated those plants. The result was the profound landscape and cultural transformation we know as agriculture.

The transition was one of the major milestones in human evolution. "I compare agriculture to bipedalism and fire," says geneticist Hugo Oliveira at the Universidade do Algarve in Faro, Portugal. "It changed completely the way we interact with the environment, the way we interact with ourselves." Agriculture is what made possible specialized professions, including art and music, and the countless trappings and manifestations of human society today, even as it also heralded such new woes as malnutrition, inequalities, pestilence, and climate change (See also this Special Feature: The Past 12,000 Years of Behavior, Adaptation, and Evolution). And once agriculture developed past a certain threshold, says Dorian Fuller, a professor of archaeobotany at University College London, UK, "there was no going back."

The precise drivers of agriculture remain a matter of fierce debate. Were people pushed into relying on plants for food because of stresses such as growing populations or climate change? Or did plants lure people in by being so abundant and useful that it made sense to turn them into dietary staples? And did religious or cultural practices, such as a tradition of providing bountiful feasts, drive the emergence of agriculture?

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Fossil evidence like this, a young pregnant adult female dating to about 6,000 years ago, suggests that as farming expanded, the health of the population declined, including more periods of poor nutrition based on analyses of teeth. Image credit: From Reference 11.

Or perhaps plant cultivation itself made those religious or cultural ideas possible (1)?

Now, some of these questions are being answered, thanks in part to the growing field of archaeobiology—the painstaking collection and analysis of tiny plant seeds, charred food or plant parts, or pieces of human and animal bones—at sites all over the world. Moreover, new genetic technologies can chart not just the genetic changes in wheat, barley, rice, oats, and other crops as they were domesticated and cultivated, but they can also identify the ancestries of the first farmers and how both populations and agriculture spread. "We are now in a real golden age for our understanding of the origin of agriculture," says anthropologist Melinda Zeder, senior scientist emeritus at the Smithsonian Institution in Washington, DC.

There are still plenty of heated controversies among archaeobiologists. "We argue about everything—the timing, the motivation, whether humans were unwitting bystanders or even tricked into it by plants," says Zeder. But a big-picture view is coming into focus.

First, plant domestication and cultivation sprang up in more places than previously thought, with the confirmed number of origin sites climbing from maybe three in the 1970s to as many as 24 today (2). Second, the past is littered with "lost" crops—wild plants that were successfully domesticated and cultivated but are not grown today. Re-run history a little differently, and we might be raising sumpweed (*Iva*) instead of corn on vast farms in Iowa (3). And third, the transformation to agriculture took place over thousands of years, with no single cause or motivation. Each crop tells its own story of a complex evolutionary dance between humans and wild plant progenitors, as both plants and humans took advantage of what the other could offer (4). "Agriculture is not a great new invention like a microchip," says Fuller. "No one discovered it, and all human society has the propensity to undertake it."

Leftover Clues

Archaeobiology involves gathering and analyzing the remains of humans and plants to discern how people were living and what they were eating and doing. It started first with bioarchaeology, a term coined in the 1970s for the study of human bones and teeth, explains Clark Larsen, an anthropologist at The Ohio State University in Columbus. Researchers can use clues in bone structure and advanced technologies to determine whether our ancestors walked or ran a lot, measure isotopes of elements such as carbon and nitrogen to gauge past diets, read ancient human DNA to chart the movements of people and populations, and spot the telltale genes of pathogens such as tuberculosis and leprosy in human remains (5).

For plant material, collected using a super-fine mesh to strain out tiny bits of char or seeds, genetic technologies make it possible to read not just entire genomes but also to determine which genes are turned on or off over the years, as the relationship between plants and humans gradually evolves, as shown by the related field of archaeobotany. "The amount of information we can obtain at the genomics and transcriptomics levels about plant domestication is absolutely mind-blowing," says Oliveira.

These technologies have helped detail not only agriculture's origins but also the intricate patterns of proliferation. The starting point goes all the way back to hunter–gatherers' vast knowledge and use of wild plants. In scanning electron microscope images, charred food remains collected from fireplaces at Shubayqa 1, a site in northeastern Jordan, show the characteristic porous structure of bread—proof that people were baking loaves from wild einkorn wheat and other plants more than 14,500 years ago, long before the first actual cultivation (6).

Then, after the unsettled and cooler climate of the Younger Dryas, the archaeobotanical records show that wild plants began to change in two remarkable ways once the climate became warmer and more stable—conclusive evidence for domestication and then cultivation. Whether wheat and barley in the Near East starting 11,700 years ago, or rice in China more than 8,000 years ago, the plants' seeds grew larger over hundreds and thousands of years. In addition, researchers have shown that, over long periods of time, more of the plant spikes had husks and seeds attached. Wild plants, of course, shed their seeds willy-nilly when ripe, forcing human gatherers to painstakingly pick them up from the ground. But as cultivation developed, the plants held onto their seeds longer—a phenomenon called non-shattering, which makes it easier for people to harvest the grain.

Both traits are believed to be unintended consequences of plant domestication. Some individual wild plants will have slightly larger seeds than others, so they will germinate and grow faster, shading out their competition. People are then more likely to collect the seeds from those plants. When humans began to save some grains to plant, fatter seeds

Wild rice (left column) contrasts with domesticated rice (right) in terms of how they grow (top row), how they are harvested (second row), and their yields (bottom row). As domestication progresses, the rice plants get taller and straighter, and more plants can fit into the same size plot, meaning they require more nutrients and water—and become more dependent on people. Image credit: Rabi Mohanty and Dorian Q. Fuller.

would lead to bigger plants, increasing the payoff. Over centuries and millennia, the grains thus grow bigger and bigger, offering humans more caloric bang for the investments they make in sowing and cultivation. "That pulls people into more cultivation because the yields are getting better and better," explains Fuller. At the same time, characteristics like non-shattering lead people to develop new harvest technologies like knives and sickles.

Needy Flora

The catch is that these changes make the crops needier. As domestication progresses in wild rice, for example, the plants get taller and straighter, as work in recent years suggests (4, 7). More plants can fit into the same size plot of ground, so they require more nutrients and more water and become more dependent on people. "I refer to it as the soil nutrient trap," Fuller says.

That, in turn, forces people to put more time and effort into cultivating the plants, leaving less time for hunting or gathering major staple foods. Fuller imagines how this could have played out at one of his study sites in the Lower Yangtze region of China, based on the archaeobotanical record. People first settle around wetlands, dining on fish, tubers, and nuts like acorns. But wild rice is there too and can be gathered and stored. To get more rice, people clear a bit of woodland or reed swamp and cast the grains to grow larger stands of wild rice. Gradually, yields and grain size increase, and harvests are easier owing to more non-shattering spikes, encouraging more investment and providing more food to fuel population growth.

But this larger and denser community then needs more firewood as well as wood to build houses and granaries. So people cut the trees that used to provide acorns and other traditional sources of wild foods, increasing the dependence on rice. Moreover, the society is forced to become more complex as people produce more, take ownership of lands, and begin to store and trade valuable resources.

Fuller's team has documented these parallel trends between 7,000 and 6,000 years ago at the Lower Yangtze site of Tianluoshan by collecting and analyzing seeds and other

plant remains at different levels (and thus of different ages) at the site. As rice seeds gradually grow in size over many hundreds of years, the percentage of rice in the diet climbs from 17% to at least 40% (and in some cases near 100% in later sites) of all the plant remains found at the site, with acorns declining and then disappearing. Tree pollen drops as the woodlands are cleared. Harvest knives and other new farming technologies appear. Populations soar as birth rates rise and more people survive to reproductive age.

By 5,000 years ago, a city called Liangzhu, with a distinctive culture, makes its first appearance in the archaeological record, with artifacts like fine black pottery, jade rings, musical instruments, depictions of "dragons," and large earthworks to control water flow. By then, "there is no way back," says Fuller. "The land is carved up into fields and there are no oaks left for acorns, which would be inadequate to support the larger population."

Cultural Impact

What's particularly exciting to researchers is that archaeobiological records are now detailed enough to begin comparing and contrasting this inexorable process of domestication and cultivation in many different locations. The decreasing dependence on wild plant foods started earlier in the Near East but took longer than on sites in China, says Fuller. One possible reason: Wheat and barley are harvested in late May, leaving plenty of time for people in the Fertile Crescent to gather pistachios and almonds at the end of the summer, while the rice harvest takes place in autumn as oaks drop acorns, leaving less time to gather nuts.

> **"Once the population began to increase and become less mobile, it sets the stage for the evolution of new pathogens, with outbreaks of new diseases." — Clark Larsen**

It's clear that people didn't just domesticate the specific wild plants that were most available; their choices reflected cultural preferences. "What we've learned is that there is a huge social component," says Zeder. For example, archaeologist Xinyi Liu at Washington University in St. Louis, MO, analyzed isotope ratios in food residues, along with other archaeobotanical methods, to figure out what people were eating for thousands of years in ancient China. In contrast to people in the Near East, who quickly domesticated wheat and barley, people in Eastern China turned to millet and rice. The difference? Liu suggests people in Western regions preferred grinding and baking, which works for wheat and barley, whereas people in eastern China liked to steam and boil their harvests, which is better for rice or millet (8). These differences can be seen in the actual artifacts—clay ovens for baking in the West and ceramic vessels for boiling and steaming in the East. "The current evidence suggests these regional differences in cooking technologies are rooted in the Pleistocene, way before plant domestication," says Liu.

Meanwhile, wild plants seized the new ecological niches created by human actions. As wheat and barley cultivation expanded in the Near East and into Europe, for example, the fields offered prime habitat for another wild plant—oats. The oats thrived amid the cereal crops—as a weed—for an estimated 2,000 years, before early farmers began to domesticate it as a crop. Cultural preferences may have been at work too, given how oats became a staple in some places, such as Scotland. "The study of weeds is still in its early days," says Fuller, "but it is one of the most exciting areas of research."

Or take squash. The wild progenitors of zucchini, cucumbers, and pumpkins contain "the bitterest chemical substances known to humans," says archaeobotanist Logan Kistler at the Smithsonian Institution in Washington, DC. Eating just a few wild plants could be fatal, and Kistler himself was shocked by the bitterness on his fingers hours after handling pieces of rind with latex gloves. Genetics reveals that only huge animals like mastodons can safely eat the squashes. Indeed, piles of 30,000-year-old mastodon stomach contents or dung in Florida reveal that the enormous creatures feasted on squash; the plants, in turn, depended on the mastodons to disperse their large, heavy seeds. When the mastodons vanished, possibly because of human hunting, squash seemed destined to fade away from the natural world.

That is, until humans did something new. They began to clear forests and build settlements. That created new "edge" environments that squashes thrive in. As a result, "the squashes shift gears and move into this habitat of humans," Kistler says. People could have first collected only the seeds or used squashes as fish floats, he suggests—just enough to start the long process of domestication and, for the squash, to act as a substitute dispersal mechanism. The central lesson: "wherever humans are interacting with the environment, the potential for domestication is there," says Kistler. Animal domestication also played a big role in proliferating agricultural economies—whether cattle and pigs in Southwest Asia, chickens in Southeast Asia, camels in Arabia, or llamas and alpaca in South America.

That doesn't mean it will always happen, though, especially where abundant wild foods are always available. "If it's a pretty good environment for hunting and gathering, why change it?" explains Fuller.

Complex Societies Bloom

Where cultivation and agriculture did take root, the impact on human history was profound. Some of the early consequences can be seen at Çatalhöyük, a 9,000-year-old Neolithic settlement in the Konya Plain of south-central Turkey. Growing wheat, barley, and rye, along with herding cattle and sheep, the population grew to a metropolis of up to 8,000 people at its peak 8,500 years ago. Archaeologists have unearthed dozens of mud-brick buildings, many built on the ruins of older ones, with hundreds of human skeletons buried beneath the floors. As the populations grew, so did the evidence for cultural or religious practices.

Analyzing the human bones and teeth, a team led by Ohio State's Larsen has shown that as the population increased and farming expanded, the health of those farmers declined (9). The patterns of tooth growth show more periods of poor nutrition, and tooth decay rises as the proportion of carbohydrates climbs in the diet. Meanwhile, changes in bone shape reveal that people needed to make daily walks to the fields, even as trash heaps and animal pens created ideal

conditions for parasites, including hookworm. "Once the population began to increase and become less mobile, it sets the stage for the evolution of new pathogens, with outbreaks of new diseases," says Larsen.

Other sites show the same trends. "There is overwhelming evidence that the risks of poor health are higher in farmers than non-farmers," Larsen says. The archaeological record also documents the rise of social and economic inequality, adds Zeder, as people shift from pooling their harvests in shared storage structures to keeping their bounty deeply buried under their own houses. Violence too rises as agriculture spreads in the Neolithic Near East and Europe, with evidence of weapons, bone breaks, and skulls bashed by rounded stones (10).

So was this shift to relying so much on plants worth it? In an infamous 1987 article, the popular historian and author Jared Diamond called agriculture "the worst mistake in the history of the human race," writing that "besides malnutrition, starvation, and epidemic diseases, farming helped bring another curse upon humanity: deep class divisions" (11).

But there was, of course, a big upside. "I do not deny that there are serious and immediate risks, like diseases," says Kistler. But without the large and predictable food supplies from farming, there would be no quantum physics, no Beethovens or Vemeers, no Great Wall or City of Lights, no airplanes or smartphones, and indeed, no modern society, technology, or culture as we know it. "Agriculture is the process that led to everything that came after," Kistler says. "We now live into our 80s and 90s and can talk through a computer—none of that is the case without agriculture."

The researchers unearthing this crucial transition say their primary motivation is to illuminate this extraordinary and complex societal transformation. But the study of the origins of agriculture could also, in principle, help feed the human populace today and in the decades ahead. Oliveira notes that only a few hundred out of more than 7,000 plants thought to have been eaten by hunter–gatherers have been fully domesticated, and only a handful—dominated by rice, maize, and wheat—provide more than 90% of the world's calories. "If we can get back to scratch and domesticate new plants," Oliveira says, "it could help feed the world and make diets healthier."

Zeder sees the work as offering important historical context for modern societies struggling to make agriculture more sustainable, even as they brace for the impacts of climate change "We have this deep, deep history of humans responding to environments and changing their environments," she says, "and for thousands of years we did take better care." Looking to the past may suggest new solutions "and hopefully," she says, "give people a sense of responsibility for taking care now."

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