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ABSTRACT

Ranging between 11,000 and 4,000 years ago, several independent origins of agriculture appeared, though scholars disagree on exactly how many. This period, known as the "Neolithic Revolution" or the "Origins of Agriculture," marks the initial emergence of food production economies. Archaeologists and biologists have worked alongside one another, often using a biogeographical approach, to investigate the origins of useful species, their range expansion, and genetic evolution through analyzing remains found at excavation sites around the world. Plant communities influence patterns in human behaviors and by understanding trends in biogeography we can begin to answer questions such as: Why did plant domestication occur where and when it did? Or, what sorts of evolution and dispersal of domesticates occurred?

Understanding patterns of plant domestication is important in understanding distribution patterns in today's society because it marks the beginning of the most significant developments in human history. Factors such as warmer climates, emergence of seasonality, and physical geography shaped the differences in threatened food security at the turn of the Pleistocene-Holocene. Hunter-gatherer societies turned to crop domestication in order to control their food supplies in a variety of ways. Regional differences in physical geography, soil fertility and local climate variations explain the emergence of different origins around the globe.

This paper is a broad review of current and past literature that has shaped our understanding of plant domestication. The research I focus on attempts to answer the question of why agriculture emerged where and when it did, and how plant domesticates subsequently evolved and dispersed. I will discuss the significance of this type of research, review some methodologies, explore incongruities in the field with regard to conceptualizations, outline the biogeography of the independent origins of agriculture, and finally the discuss the human ecology of agricultural societies.

INTRODUCTION

Archaeologists and biologists have worked alongside one another, often using a biogeographical approach, to investigate the origins of useful species, their range expansion, and genetic shifts through analyzing remains found at excavation sites around the world. Understanding the natural history of plants as they relate to hominid species is important in understanding biocultural patterns in today's society. For example, analyzing historical changes in plants correlated to climactic shifts can predict how our relations with plants might be altered over the course of current climate changes.

Plant communities influence patterns in human behaviors and by understanding trends in plant domestication we can begin to explain some of these trends (Gremillion 1997). Price (2000) insists that "the transition from hunting-and-gathering to agriculture is…the most important event in human prehistory, representing a shift from foraging to farming, from food collection to food production, from wild to domestic, that sets the stage for most of the significant subsequent developments in human society."

One of the major transition periods in human history began between 11,000 and 9,000 years ago. This period, known as the "Neolithic Revolution" or the "Origins of Agriculture," marks the initial emergence of food production economies. Agriculture-based societies pressured populations to limit mobility, which previously characterized the hunter-gatherer lifestyle. The cooperation required and food security provided with this lifestyle shift stimulated a significant population boom and extensive landscape alterations. The emergence of permanent settlements allowed for the construction of building to inhabit, house domesticated animals, and protect agricultural crops. The tower of Jericho, in the Jordan Valley, being one of the more famous examples, was likely built to protect agricultural fields from floodwaters (Smith 1995). In many ways, these foundational changes directed the course of human societies; our current economies are still centered on agriculture as our primary subsistence.

Western institutions, touting specific technologies and methodologies, have conducted the vast amount of research in plant domestication. Is it because we are fascinated by the intimate relationship with nature that once existed in our evolutionary and societal past? Something draws us to "primitive" societies in which dynamic plant-people interactions dictated the lives of our ancestors in very complex ways. Now, a new discipline of human ecology is emerging in search of "rediscovering" a mutualistic relationship with our surrounding. In part, this is arising out of necessity and insuring survival of our species in the face of an unknown future. Global changes in weather patterns, plant dispersal, and human health threaten the lives of millions of humans. Perhaps we have reached the dusk of the Holocene period and not unlike our

ancestors, we will be forced to dramatically alter our lifestyles to accommodate for these rapid changes. Biogeographic knowledge of plant domestication can help direct the ways we may adapt our lifestyles to accommodate for these imminent changes.

METHODOLOGIES

In this section, I will outline a variety of archaeological methods of studying plant domestication such as molecular analysis, fossil remain interpretation, and artifact examination. Evidence arising from this type of data extraction can be pieced together using biogeography to interpret the significance of local findings. In this manner, we can start to concretely answer biogeographical questions such as where did domesticates originate, why, and how did they spread or evolve?

Until recently, there was no universally accepted methodology of paleoethnobotanical research—the study of historic human use of plants—causing some researchers to call for a more cohesion across the discipline in order to unify the field. Lennstrom (1995) encourages developing a "systematic recovery and analysis" of plant material remains to unify methodologies across the discipline in an economically feasible manner. Cross-disciplinary methods can help eliminate interpretation and sampling biases.

Research progresses from field collection, species descriptions, remain collection management and describing patterns yielding clues about the origin of human-plant interaction. In biogeography, it is always a challenge designing an international strategy so that data coming from all parts of the world would be compatible and accepted by colleagues. Some problems that have arisen in the past are inconsistencies in excavation and collection from archaeological sites biasing distribution results. Furthermore, classification and quantification are associated with many challenges including fragility and variable specificity of identifying remains (Hastorf 1988). Research can be categorized into categories of genetics, fossil remains, and secondary evidence from artifacts.

Genetic Analysis

Some scholars assert that domesticated plants cannot survive in the wild without human intervention and therefore domesticated traits in wild populations are likely to be transient. However, *cultivated* species may or may not become dependent on humans for reproduction and may or may not be viable in a given environment without human interaction (this will be addressed in depth in the next section). It is possible for a species in a given geographical

extent to become completely dependent on human intervention for reproductive success while remaining "wild" in other parts of its range. Plants that have been domesticated can occasionally "escape" and hybridize with naturally selected plants and perhaps be redomesticated from this new gene pool. This process can occur any number of times adding to the plant variety, genetic drift, and spatial heterogeneity. The chromosome count in a given species can predict the hybridization history. For example, it is likely *Triticum monococcum* (einkorn), the first wild wheat to be extensively cultivated, likely hybridized with wild species multiple times, undergoing polyploid chromosome pairing, until *T. aestivum* (modern bread wheat), with 48 chromosomes, came about (Cox and Moore 2005).

There is a lot of information available through genomic analysis that is not apparent by physical examination of remains. Genomics has greatly enhanced our understanding of the causes and consequences of the Neolithic Revolution not only by providing clues about the patterns of plant domestication, but also revealing information about the emergence of pathogens and parasites around this time. Furthermore, we can begin to measure shifts in the human genome coming out of agricultural lifestyles. The spread of plants and the locations of these processes can be better understood through this approach. Armelagos (2005) found that pathogens thought to have emerged during the foundations of farming were actually present in foraging societies as well. There is evidence that humans were a source of transmission of some parasites to domesticated animals rather than vice-versa as previous models predicted.

This type of molecular analysis assists biogeographers in developing theories of the origin and consequences of agriculture practice. We see specific physiological traits that correspond to plant domestication. Furthermore we have learned about mechanisms for dispersal and the impacts on human populations. Now we turn to macroscopic evidence to further clues that aid in assessing the biogeography of plant domestication.

Archaeological Plant Evidence

One commonly utilized technique is analysis of microfossils such as phytoliths, pollen, and starch grain remains. Microfossils can yield important clues as to agricultural origins, Pleistocene/Holocene environmental changes, and the evolution of slash-and-burn agriculture (Piperno 1998). Phytoliths are rigid, microscopic plant parts usually made of silica or calcium oxalate and therefore do not decay. Strengths of a given type of plant microfossil analyses can supplement weaknesses in other methodologies, contributing diverse clues to the larger picture. Phytoliths can be extracted from dental remains or food processing tools and reconstructed to identify a floral species when the rest of the plant has been burned or rotted away. Pollen

palynology involves chemically extracting pollen (and other microscopic organic material) out of sediment core or rocks. Other microfossils, such as starch grain fragments, can be recovered from fire remains or fossilized human feces.

Another method is to analyze macro remains through flotation, among other techniques. Flotation is a technique used to extract tiny artifacts from soil from archaeological sites. Water is bubbled through dried soil and seeds allowing charcoal and other light materials to float off and be collected separately from heavier materials such as microliths and bone fragments (French 1971 and Struever 1968). The flotation method of extracting plant remains not only helps to understand domestication and subsistence, but to study the spatial variability of plant remains allowing for the development of cultural context (Lennstrom 1995).

Radiocarbon dating is a common way to analyze macro or micro plant remains. It is important to note one problem with this method is the variant levels of atmospheric carbon in the atmosphere can skew the results of the carbon-14 determined age. Thus carbon dates should be (but are not always in literature) corrected based on the known levels of atmospheric carbon in a given era so dates are not divergent from real-time (Smith 1995). In recent years, estimates have been adjusted to accommodate for the greater accuracy provided by new technologies, frequently challenging previously held notions regarding the origins of agriculture.

Just as taxonomic inflation and other systematic disputes affect research today, we should also keep in mind that plant fossil remains can also be interpreted differently. Percentage distributions are useful to compare the relative abundance of different taxa at a given location. Density values are useful in comparing the relative abundance of a single taxon at multiple locations (Lennstrom 1995).

In combination with molecular techniques, macroscopic evidence further helps us piece together the biogeography of plant domestication, as proceeding sections of this paper will attempt to synthesize. At an even larger scale, we now look at the value of artifacts in telling the story of plant domestication.

Archaeological Non-plant Evidence

Information can also be derived through interpretations of secondary resources. Another method, which highlights the creativity of some archeologists, involves examining cornhusk and seed impressions in ceramic remains. In one specific example, Eubanks (2001) used this method to identify the variety of species of maize used by ancient cultures in Mesoamerica. In addition to clues about plant domestication, these relics point to cross-cultural exchange of maize species and even depict ceremonial dress involving the multipurpose crop. In all,

Eubanks identified 16 distinct maize races on 129 ceramic remains from Peru and Mexico. Eight of the same races appear in both places.

Seeds remaining in baskets or other containers are sometimes in well-preserved conditions and provide evidence of collection and storage of certain species. The structure and composition of tool remains can also indicate something about how agriculture was first practiced and where and how its knowledge was spread.

Finally, analysis of remains found in fossilized human feces is a way to prove without a doubt what plants were consumed by humans, in what proportions, and whether the given species shows traits of domestication (discussed in previous section) or whether it was a wild-type that was gathered.

The extent each of these methodologies should be used is determined on a case-by-case basis. It is impossible to say one methodology is better than another, because, as you will see evident later, no method is superior across every situation. Furthermore, due to differences in preservation quality across sites, options of which techniques to use can be highly variable. Used in combination as quantitative evidence can help support macro-theories of biogeography in the patterns of plant domestication.

Biogeography plays an important role in piecing together concrete evidence from around the world, from different time-periods and geographic locations, to answer questions regarding the origin of agriculture. The methods outlined above must be integrated with broader perspectives, and theories, discussed below, in order to understand when, where and why plant domestication emerged where it did and its subsequent evolution and dispersal.

PLANT DOMESTICATION

"Domestic races of animals and cultivated races of plants often exhibit an abnormal character as compared with natural species; for they have been modified not for their own benefit, but for that of man." —Darwin (1868) The Variation of Plants and Animals under Domestication

Throughout this section of this review paper I will highlight prominent literature debates, ongoing discussions, and interdisciplinary perspectives. Three problems dominate the discourse I found in my research: 1) which came first, domestication or cultivation, 2) what is the difference between foraging and farming, or can such a distinction even be made, and 3) why did agriculture arise where and when it did? Exploring these questions is important in shaping

the biogeographic story of plant domestication because they consider the mechanisms of the societal transition that took place during the Neolithic Revolution.

Which came first, domestication or cultivation?

First, it is important to define the terminology used throughout this paper because concepts are still loosely defined, sometimes highly debated and can be rather ambiguous with multiple definitions. According to Blumer (1991), "'Domestication' is the evolutionary process whereby humans modify, either intentionally or unintentionally, the genetic makeup of a population of plants or animals to the extent that individuals within that population lose their ability to survive and produce offspring in the wild." Domesticated plants tend to lose certain traits maintained in wild progenitors such as dispersal mechanisms, chemical and physical defenses against herbivory, and dormancy (the vast majority of economic plants today are annuals). 'Cultivation' refers to the unintentional evolution of plants for the benefit of humans and the subsequent harvest. Throughout this paper, "domesticates" will refer to plants whose origin or selection is primarily due to intentional human activity, and which cannot survive and/or reproduce on its own (Spencer 2007).

The question remains, which came first, cultivation or domestication? Ladinsky (1987) asserts that domesticated traits arose due to hunting-gathering pressures. He used mathematical models to show high-pressure demand on the seeds of lentil (*Lens culinaris*) led to dormancy-free species. This calculation however is highly criticized and not widely accepted (Zohary1989). Blumler et al. (1991) refutes this argument, declaring instead that "cultivation sets up selection pressures that favor the evolution of domestication even if humans do not consciously choose to plant individuals with the domesticated phenotype." In this mechanism, wild progenitors were gathered, stored, and processed resulting in subsequent domestication.

This offers one possible origin of domesticated crops, though the possibility that people accelerated evolutionary change through intentional selection should not be ruled out since it is likely domestication occurred faster than "natural selection" which can be weak and unpredictable. For example, Blumer (1991) outlines the possibility that harvesting wild cereal plants can lead to an increased frequency in which grain spikelets remain on the rachis as opposed to wild-type spikelets that fall off when ripe. In legumes seed pods remain closed rather that dehiscing to disperse seeds. These are human favored phenotypes and characterize many domesticated crops today. Sometimes these traits can be discerned based on fragmentary remains from archeology sites, yielding clues about which plants were domesticated when.

Before plants were intentionally planted, it is likely some of their wild-type predecessors were gathered, stored and processed due to similar climactic instability. For example, wild grains, grinding equipment, and a stone oven were excavated in 2004 from Israel's Sea of Galilee. Archaeologists found 143 varieties of seeds, including wheat and barley, dating back over 23,000 years. Researchers suggest they did not actually plant crops but rather a cooling period and disappearance of wild game forced these Ohalo people to gather seeds in the fall, grind them into flour and bake the food source to survive winter months (Zorich 2005).

As we saw in this section, the mechanism of the emergence of agricultural crops was likely a combination of both intentional and unintentional cultivation and domestication, though intentional selection by humans seems more plausible as the primary driving force behind the evolution of plant domesticates. As we will learn in the following section, human behavior changes are complex as well, and not at yet fully understood. However, this type of research is important in understanding the biogeography of plant domestication and subsequent influence on human societies.

The transition from foraging to farming

It is impossible to point to an exact moment when plant domestication occurred because it was more than likely a gradual shift with combination societies in between transition periods who both foraged and farmed. Perhaps farming and foraging were not so dichotomous but rather located on a spectrum depending on "the intensity, intentionally, species focus, and total range" of a societies interventions with plant species' life cycles (Smith 2001). In fact, Terrell (2003) argues the search for the "origin of agriculture" is outdated terminology and actually inhibits objective reasoning about the history of plant domestication. Instead, he argues 1) domestication should be measured by its conduct rather that its consequences, 2) a plant could be considered domesticated where and when and species knows how to harvest it, and 3) human domestication of a species varies depending on how much is wanted in a given season. Conventionally, domestication is used to refer to intentional or unintentional permanent genetic or morphological modification of a species by human selection and harvesting. Terrell suggests we should qualify domestication as a species that could be repeatedly exploited by people in one or more places.

We cannot think of plant domestication in isolation; we must also consider landscape domestication. The concept of species adaptation is somewhat of a misnomer because "organisms not only adapt to environments, but in part also construct them" (Odling-Smee *et al.*, 1996). Since humans significantly alter the geology, flora, and fauna in combination with one another, domestication is more complex than at the species level. Ingold (1996) observes that

humans do not actually create a domesticated species, but rather "[establish] the environmental conditions for their growth and development." Thus, the differences between foraging and farming are based on the extent to which humans are involved in establishing the conditions for growth and reproduction.

Human alteration of landscapes for plant domestication is thus varied and an exact point of "domestication" cannot be clearly defined. However, as discussed in the methods section, there is obviously conclusive evidence indicating plant domestication. In the following sections of this paper, I will review literature that attempts to explain why these transitions occurred where and when they did, and the emergence of a different kind of economy. As discussed in other biogeographic topics, similar abiotic (i.e. climate, soil fertility, and physical geography) and biotic (i.e. overkill, ecosystem shifting, and competition) also influence spatial and temporal patterns of plant domestication.

Origins of agriculture

There are many benefits to developing plant domesticates including predictable and reliable germination rates, reproducibility of plant species, higher caloric content in edible parts, and reduction of toxic allelochemicals, to name a few. But the questions that continue to perplex paleoethnobotanists, archeologists, and biogeographers are why did plant domestication occur where it did and when it did? Why did agriculture emerge independently in some regions of the world and not in others? What led hunter-gatherer societies to make the transition to an agricultural way of life? These questions must be addressed through multiple disciplines, integrating discoveries of biologists, archaeologists, and historical anthropologists to piece together the origin of agriculture (Smith 1995).

First, it is important to note that humans in foraging societies should not be viewed as passive participants in the ecosystem. Hunter-gatherers took many actions to secure their food source and increase their chances of survival. In fact, some scholars insist the origin of agriculture should not be viewed as an act requiring any new facts of knowledge due to the assumption that people of even strictly hunter-gatherer societies still posed ecological knowledge regarding patterns of germination, seasonality, soil and precipitation conditions required for certain plants (White 1959). Hence the term agriculture refers to the rise of a "new kind of relationship" that came about when the hunting-and-gathering no longer provided sufficient resources for a population. Studies have shown that gathering can actually be more energy efficient than cultivation under the right conditions (Harlan 1975). Our human ancestors had been hunter-gatherer societies for millions of years before, which leaves us to assume agriculture emerged out of some kind of new necessity that emerged during this period when

only gathering food was no longer a reliable source. This change could have occurred due to either population growth or shortages of food for one reason or another. Thus, humans instated measures to control food sources through domestication.

There is evidence of plant domestication occurring independently in several places around the world during the end of the Pleistocene. By the 1940s, Nikolai Vavilov had identified seven distinct regions based on genetic evidence of existing plants. These regions, described in greater depth in proceeding sections of this paper, include the Fertile Crescent, north-central Africa, two regions in Asia, Andean regions in South America, Central America, and northeast North America. He reasoned that the higher the phenotypical diversity of an agriculturally significant plant species, the longer it has been optimized by humans, and thus, the more likely it indicates a distinct region of domestication. In the 1950s, Braidwood used an archeological approach by investigating remains at various excavation sites around the world and found much overlap with the biological evidence uncovered by Vavilov. For the most part, scholars today still recognize these regions as Origins of Agriculture.

In foraging societies, small, familial groups were maintained to maximize efficiency and since there is no evidence that space was limited, it is unlikely plant domestication arose due to population pressures. As evidence, we know settlement in the Americas was relatively recent occurrence compared to the Old World, and therefore does not provide a good argument for plant domestication coming about due to population or space pressures. Furthermore, due to limited mobility of primitive cultures, it is unlikely ideas were spread via intercultural communication but rather came about because of changes in the environment.

Domestication of plants occurred at the end of the Pleistocene due to changes in plant communities and changes in human behavior, perhaps a result of unpredictable climactic shifts. Seasonality, rainfall, mean annual temperature, and atmospheric CO_2 began to change during this period. Byrne (1987) suggests a distinct pattern of seasonal rainfall arose during this period, which encouraged the growth of annuals and geophytes (energy storage organs in plants offering nutrient rich food sources for animals, including humans). Other climactic changes threatened food security of hunter-gatherer societies inciting cultivation of plants in an attempt to control a source of reliable subsistence. Farmers had a competitive advantage and thus societies quickly transitioned from hunter-gatherer lifestyles (Diamond 2002). Other theories predict grasses, such as wheat and barley, may have moved north during the warming climate, taking advantage of settlement disturbances and clearings. Inhabitants then would have realized the nutritional value of these species and began cultivating them. Finally, the overkill hypothesis could be interpreted, as a factor that caused hunter-gatherer societies to turn

to domesticates as their primary food source, though there is surprisingly sparse literature addressing this possibility.

Plants were never developed for harvesting in other geographic regions such as Southern Africa, Australia, California and southern South America. What hypotheses exist that could explain these patterns? Climactic factors also limited the extent to which certain early cultivars could be used as crops predicting why cultivation occurred in some regions and not others (Cox and Moore 2005). Other factors such as physical geography can influence patterns of rainfall, water availability, drought, and flooding that would influence which crops were developed where. Soil fertility based on previous climactic and tectonic activities also determined where agriculture was viable. Additionally, there are factors influencing availability of information and research trajectories that likely alter the outcome of conclusions regarding the biogeography of plant domestication.

The following section will flush out the seven regions around the world currently recognized as independent agricultural origins. Articles under review will discuss which crops were among the first domesticates of each region, explore what factors influenced the shift from foraging to farming, and describe subsequent changes in human societies inhabiting these regions at the time. Plant domestication is different from region to region but certain biogeographic theories emerge to explain the Origin of Agriculture.

INDEPENDENT AGRICULTURAL ORIGINS

Independent centers of domestication are identified through both spatial and temporal contexts. These centers are characterized by maximum of genetic diversity for crop plants (Smith 2006). The following sections will outline plant domestication from several accepted independent agricultural origins: the Fertile Crescent, Europe and Africa, East Asia, Middle and South America, Eastern North America and the Southwest (listed in chronological order based on dating of fossil records.) Methodologies outlined above and the theories discussed in previous sections are applied to the following investigation of independent origins of agriculture, demonstrating how concrete evidence and biogeographic theory can be built upon one another to tell the story of plant domestication. Examples from excavations, genetic analysis and carbon dating are provided and though these reviews are not comprehensive, each section is intended to demonstrate how complex research can be pieced together using biogeography to predict patterns of the origins of agriculture.

The Fertile Crescent (10,000 ybp)

Domestication of cereal crops such as barley, emmer, and eikhorn wheat likely began in the Fertile Crescent circa 9000BCE. This part of the Middle East, curving from the Mediterranean coast in the west to the Zagros Mountains in the east, has a climate that favors the evolution of certain types of nutrient bearing plants. Large-seeded annual plants, such as peas and wheat, readily evolved in warmer wetter climate characterizing the end of the Pleistocene ice age. The expansion of grasslands invited wild game to proliferate providing abundant food for hunter-gatherer in addition to the wide variety of wild grains.

These societies likely practiced vertical transhumance in which they moved to higher elevations during the summer to harvest wild grains while they stayed in lowland areas to hunt game in the winter months. The elevation difference in the region also aided the development of a variety of potential grains to harvest. Overtime, the next 2000 years, these societies settled into permanent villages, depending on domesticated plants and animals for subsistence. Utility of some of the methodologies discussed earlier in this paper, help piece together the story of emmer wheat, einkorn wheat and barley and further contribute to the biogeographic questions of plant domestication in this region.

- Emmer Wheat (*Triticum araraticum)*

  This domesticate is an example of a species that is morphologically indistinguishable from Timopheev's wheat (*Triticum araraticum*) which was originally thought to be the wild progenitor of emmer wheat. In this case, we see the importance of genetic analysis in order to distinguish these species (which cannot hybridize, as previously discussed, but do occur in the same geographic region).

  Physiological changes in the wheat are good indications of when the grass was domesticated. When emmer was domesticated, the grain became larger and the rachis less brittle (so seeds were not easily lost before the harvest). These changes are good indicators of increased human selection of this species, driving evolution so the wheat was increasingly beneficial to societies in the Fertile Crescent.

- Einkorn Wheat

  Drawing on the cultivation vs. domestication argument presented earlier in this paper, there is evidence that einkorn wheat was harvested by hunter-gatherer societies before it was domesticated. Through fossilized fecal analysis, einkorn wheat appeared in known hunter-gatherer societies, among one of the earliest known grain consumed by these cultures (Hillman 1990). Recent research on this grain in particular indicates it has very high yields in a relatively short period. Harlan (1972) estimates after three weeks of

harvest of the wild einkorn wheat, a family of four would have enough grain to sustain them for a year.

- Barley

  Unlike the two wheats discussed above, wild progenitors of barley are found through the full extent of the Fertile Crescent. Two morphologies are found in combination together and with emmer and einkorn wheat at various locations across the Fertile Crescent. Like its wild progenitor, there is a two-rowed variety with two vertical rows of grains while a second variety contains six, presumably an adaptation to increase the chances of being selected for planting by humans. This type of adaptation is a common trait of domesticated crops.

The Fertile Crescent is one of the more famous regions of plant domestication due greatly to the vast extent of the resources directed at excavation and research. Skeptics point out the fact that the majority of long standing grants and researchers are located in Europe, and the natural history of one's particular agricultural patterns is of particular interest which may lead to a somewhat skewed emphasis on the importance of the Fertile Crescent, possibly overlooking the full significance of other agricultural origins.

As discussed earlier, research in the Fertile Crescent utilizes genetic and morphological research extracted from fossil and fecal remains to contribute quantitative information about plants used by cultures in the Fertile Crescent 11,000 years ago. Patterns of human behavior (i.e. cultivation vs. cultivation, foraging vs. farming) build upon this evidence and the story of plant domestication in the Fertile Crescent emerges, providing a model for comparison against other independent origins.

Europe and Africa (4000 ybp)

The spread of agriculture out of the Fertile Crescent was limited by the Sahara and by cool climates in Europe. Genetic analysis can definitively assert multiple centers of domestication. These types of results are particularly powerful when they indicate paralleled domestication of both animal and plant species. This type of research is limited in that wild progenitors may not exist in former ranges. But establishing the relative timing of domesticates from different regions can hint to possible origins or expansions. Though they may have emerged independently, this type of evidence is important to consider.

Societies in southern Europe may have learned of agriculture in the Fertile Crescent via extensive trade routes rather than western migration. Excavations of the Franchthi Cave in

southern Greece launched by T.W. Jacobsen provide evidence of both wild and domesticate plants appearing simultaneously; indicating the origin of agriculture was a slow transition rather than something abrupt (Muller and Chapman 1990). The 7000-year-old Passo di Corvo settlement of southern Italy consists of a series of ditches and walls containing evidence of both housing for people and herds (Geddes 1985).

Poor preservation, difficulty in material recovery, and very little research commitment in sub-Saharan Africa have contributed to the limited information we have regarding early origins of agriculture in the region. It is suggested that seed crops (wheat and barley in Europe and rice, millet and sorghum in Africa) were domesticated sometime after inhabitants started herding animals. A model of mixed forage/farm economies was likely. The key to agricultural success in part of this region (sometimes with a relatively less favorable climate) was farm placement. Scattered, wind-deposited soils that were fertile, well drained and easily tilled were essential to farming success in temperate areas in Europe. Similarly in Africa, fertile grasslands were previously present in what is now the Sahara (7,000-4,000 yrs ago) where evidence of many settlements can be found (Clark and Brandt 1984). Finally, an interesting difference to not in this region is the evidence that early African agriculture technologies utilized iron as opposed to lithic tools found in many other centers of origin (Bower 1995).

As we have seen in this section, though preservation and knowledge is poor, archaeologists and biologist combined molecular and fossil evidence in addition to landscape alterations to build upon theories behind plant domestication in this region. Similar to the Fertile Crescent mechanisms such as climate change altered the seasonal behavior of these populations but agricultural behavior was limited in this case by relatively cooler and physical barriers such as the Sahara desert and poor soils.

East Asia (8,000 ybp)

Eastward from the Tibetan Plateau, forest gradually gave way to agriculture around 7000 years ago. Archaeologists have identified two distinct regions of domestication based on different east-flowing river systems in present day China: the Yellow River of the north and the Yangtze to the south. Differences in climate due to weather patterns and physical geography such as the Ch'in Ling mountain range influenced the plant domestication in geographically distinct ways. Thus, two importance crops, millet and rice, were domesticated in two distinct regions due to their different climactic requirements.

- Rice *(Oryza sativa*)

Rice crops require landscape alteration in the form of dikes in order to form paddies. Hunter-gatherer societies likely had to establish permanent settlements to tend such transformations. Converting dry land into seasonally flooded areas would have allowed increased yield and heightened control over rice varieties. In the Yangtze River valley during the Late Pleistocene, the climate was cooler and drier than today's climate and *Oryza sativa* may have been natural component of the vegetation but was probably not well adapted to the glacial climates. In contrast, in the early Holocene, the climate was likely wetter and more seasonal that at present, and rice may have been distributed further north. Other factors such as atmospheric CO_2 levels may have influenced the extent to which human's were able to exploit wild *Oryza* (Zhao 2000). Further carbon dating of a significant volume of stalks, leaves, and husks of domesticates establishes the earliest known rice cultivation occurred in the region dating 6500-6000 years ago (Smith 1995).

- Millet (*Panicum miliaceum* and *Setaria italica*)

  Further north, along the Yellow River where millet crops dominate, the climate is characterized with seasonal flooding and drought. Millet as a drought-resistant crop thrived here where rainfall was marginal whereas rice dominated the Yangtze River valley, which is subject to fewer droughts and floods and has a humid, precipitous climate. Early settlements are found between the semi-arid highland foothills of the Tai-hang Mountains to the west and the deciduous forest of the plains to the east. Excavations of these settlements reveal storage pits containing grain remains as well as tools such as stone axes (for forest clearing), stone hoes (for tilling oils) and stone mortar and pestles (for grinding grain).

Unique aspects of the settlements in this region allow archaeologists access to a lot of well-preserved information. Many tools among other clues in this region were extracted from burial mounds. Peat bogs, present in this area, are infamous for slow decomposition rates and as a result provide great opportunities to excavate well-preserved remains from ancient civilizations utilizing methods of study with which we are already familiar. For example, remains of digging implements were recovered from the Ho-mu-tu peat deposits near Hang-chou Bay, likely used for preparing rice paddies (Wenning 1991).

Asia provides a good example of human behavior-change shaped by plants' needs, as discussed earlier in the paper. Extensive landscape alteration (tool artifacts and evidence of paddies) was directed by the type of crop most viable for the given region. In this manner we

see how biogeographic processes drove developmental differences between these different regions of agricultural lifestyles. Simultaneously we see similarities to the other regions discussed in that warming and seasonality arose, demanding hunter-gatherer societies shift toward sedentary economies.

Middle and South America (4,500 ybp)

Utilizing the ice cap covering the Bering Strait, humans moved from Siberia to Alaska around 20,000-15,000 years ago. As the Pleistocene ended, bringing warmer, seasonal patterns of climate characteristic of the Holocene, hunter-gather societies began to adjust to the changing plant and animal communities. The Incan, Mayan and Aztec states flourished in the Americas as well-established, productive agricultural economies with extensive technologies and infrastructures. Crops were focused on squash, maize and beans. In tropical lowlands of South America manioc (*Manihot esulenta*) and sweet potato (*Ipomeoea batatas*) were the principle domesticates. Case studies of maize, bean and squash domestication in South and Central America follow:

- Maize (*Zea mays*)

  Modern ears of corn are morphologically highly variable due to thousands of years of human selection in different geographic regions. Based on radiocarbon dating and fossil remains, archaeologists have concluded domesticated corn spread from Mexico southward into Central and South America. Its ancestor, Teosinte, had numerous, smaller stalks each having several small grain spikes which evolved into a single stalk with a few easily harvested cobs containing seeds which could not be dispersed independently (Doebley 1990).

- Beans (*Phaseolus vulgaris*)

  Today, the wild ancestor of beans grows in a broad range and thus it is hard to locate where the cultivar originated. However, wild cultivars and crops today have distinct varieties of the protein, phaseolin, present in the seeds and based on this information it is possible to identify two different origins (Gepts 1990). It is thought that this species was independently domesticated in both Mexico and in the southern Andes. Due to a 2400-year gap in the evidence of maize and bean domestication, it is not likely in early history that the two crops were domesticated together.

- Squash (*Cucurbita pepo*)

  Squash is much less extensively studied; limited research is available regarding the distribution, dispersal and origin of squash varieties. Part of the complication is the

rich variety of the species ranging from pumpkin, acorn, zucchini, marrow, spaghetti, and patty pan. Because of the diversity of wild progenitors that grow today of at least three of these varieties, it is thought to have originated in South America. Three types of squash seed recovered from Ocampo caves in Mexico were deemed large enough to be from domesticated varieties dating back 9000-7000 years ago (MacNeish 1958).

Similar to peat bogs in Asia, caves in this region are promising locations to continue looking for evidence of crop domestication due to the sheltered environment which both preserves remains and were highly utilized by societies as shelter and food storage. Seasonal occupation is evident in the La Perra Romero caves in Mexico reflecting the climate at the time and providing an interesting case study of the initial transitional period between hunter-gatherer lifestyles and the first cultivations (MacNeish 1958). It would be expected that domestication patterns between species is often parallel, reflecting shifts in societal patterns in accommodating for holistic nutritional needs.

Though patterns of human settlement (mostly in caves) are different than other regions discussed, similar biogeographic theories and methodological techniques support a unique but parallel story of plant domestication. Quantitative data derived from morphological evidence of domestication and molecular analysis from artifact remains, lead researchers are to conclude similar mechanisms of seasonality and warming vastly drove domestication even though this region doesn't show evidence until a few thousands years after the turn of the Pleistocene.

North America (4,500 ybp)

Maize spread northward as well into what is now the heartland and eastern deciduous forest of the United States where cultivation began around 1-200 AD. Maize does not tell the story however of an independent center of domestication, where agricultural societies flourished 2000 years before maize arrived. Both cave and river valley settlements have provided evidence in the form of seeds preserved in caves, carbonized by fires, or recovered from a woven basket that indicate to archaeologists an independent origin of goosefoot (*Chenopodium sp.*), a variation of modern quinoa. Researchers believe *Cucurbita pepo* was also independently domesticated in North America (Smith 1994).

The status of eastern North America as an independent center of plant domestication has recently been called into question, based on genetic evidence that species may have originated in Mexico. In addition to dating archeological finds, genetic analysis of fossils remains an important way to determine if and where domestication occurred in independent

regions around the world. Smith (2006) defends the northeast's standing based on extensive genetic evidence from four different species: marshelder (*Iva annua*), chenopod (*Chenopodium berlandieri*), squash (*Cucurbita pepo*), and sunflower (*Helianthus annuus*).

- Marshelder (*Iva annua*)

  Though it is no longer cultivated today, this plant plays an important role in establishing eastern North America as an independent center of domestication. Though its wild progenitor exists in Mexico and North America today, there is no evidence of domesticated use of marshelder in archaeological sites in Mexico, whereas there are remains found in settlements in North America (Smith 2006). No one disputes that this region had early agriculture but some scholars have challenged its status as an independent region, saying that domesticates were transported northward (Wilson 1990).

- Chenopod (*Chenopodium berlandieri*)

  Still cultivated in Mexico, wild progenitors exist in both Mexico and North America today. The supporting evidence this plant, commonly known as goosefoot, provides is through the morphology of its seeds. A thickened testa or seed coat, for better storage capabilities, allows it to be distinguished from its wild ancestors (Smith 2006). Again archaeological evidence for domesticates is lacking at any sited in Mexico until the 16th century. Furthermore, genetic analysis found significant differences between wild progenitors in North America and the line cultivated today in Mexico (Ruas et al. 1999). Further tests between wild progenitors and domesticates in both regions should be compared.

- Squash (*Cucurbita pepo*)

  Two distinct lines of domesticates arise from this species—pumpkin and squashes in the subspecies of acorn, crooked necks, and scallop. The second is thought to be an independent domesticate of eastern North America due to molecular evidence indicating the wild progenitor is most likely native to eastern North America and is not found in Mexico (Emschwiller 2006). Morphological evidence (larger seeds, fruits and peduncles) is found in both regions under question (Mexico and eastern North America), which closely overlap the range of distinct wild progenitors. Thus it would make rational sense that each line of *C. pepo* was domesticated from the geographically correlated progenitor.

- Sunflower (*Heliathus annuus*)

In 1951, Heiser was the first to propose the sunflower was an independently domesticated crop in eastern North America and subsequent archaeological and genomic evidence emerged out of proceeding research to support this hypothesis. One such study studied an extensive number of alleles of samples across the continent from both wild progenitors and current domesticates, concluding domesticates today have significantly lower diversity than wild progenitors (Harter et al. 2004). Furthermore, domesticates show greater similarity to North American wild species, thus if seeds from the sunflower are found at sites in Mexico, this would imply either a southward migration or independent domestication depending on the genetic composition.

Evidence in the Southwest is severely lacking in many respects and it is even more likely that remains from settlements were carried by humans there. Particularly, there has been no evidence of non-brittle rachises, increase in grain, or loss of glumes, which can be found in other independent centers such as the Fertile Crescent (Wills 1993). The wide variety of landscapes and ecosystems in a relatively small area provides an interesting area to study the adoption of agriculture and the addition of domesticates to foraging economies. In this region, water was a limiting factor in the production of cultivars, though there is evidence of use of arroyos to direct groundwater for maize cultivation.

In order to piece together history based on evidence from both the past and present (historical biogeography) we must understand ways plant ecology and evolution can change over time. As discussed throughout this section, plant domesticates can disperse via a variety of mechanisms. We see human-initiated dispersal as a primary method through trade (Europe) or migration (Mexico to eastern North America). Plants can also disperse through traditional ecological methods like wind or animal. We saw in previous sections how genetics can change as well through hybridization with wild varieties. Furthermore, genetic drift or other evolutionary mechanisms can drive changes in plant range and genetics.

Biogeography is vital to in order to develop widely applicable theories that emerge through assessing the similarities and differences between these independent origins of agriculture. Biogeography aids in answering the questions of why did agricultural patterns of human behavior emerge when and where they did. Additionally, we see disparity in plant domesticate distribution and expansion based on regional differences in climate and physical geography.

Understanding the biogeography of plant domestication is important to understanding human relations to ecology, that is to say, human ecology. Changes in human behavior during the Neolithic Revolution are still evident today in our current economy. In the face of growing population pressure, climate changes, and environmental degradation, biogeographic knowledge of plant domestication has important application in today's world.

HUMAN ECOLOGY: PLANTS AND PEOPLE TODAY

Not only did the Neolithic Revolution bring profound changes in economic innovation, but also increased population, caused social reorganization, and added new types of technology. Changes in human demography, health, and diversity in turn shaped the relative dominance of certain cultures, genes, and languages, forever changing how humans relate to the natural world. It was this era from whence intensive commodification of the environment began (Twiss 2007).

People adjust their behaviors and actions to fit the ecology of plants under domestication. For some species of plants, human's adaptive skills and tactics may require greater environmental manipulation and alteration. Thus, human subsistence behavior should be described in terms complex interaction between harvesting tactics and the species under consideration (Terrell 2006).

Niche construction is a term applied to efforts of environmental modification that, in theory, enhance the world for ourselves, improving our quality of living and chance of survival (Smith 2007). We have used our impressive engineering skills to alter our environment to an extent that, as we now know, may actually threaten our survival. The niche construction behavior associated with the beginnings of domestication has been greatly magnified over the past 10,000 years and is reflected in today's societal organization.

Today, our agriculturally adapted lifestyles and food security are threatened by climate change, increasing population pressure, and widespread environmental alterations. Human behavior is subsequently adapting to address these pressures. Genetically modifying crops, developing methods of biocultural conservation and integrating the value of ecosystem services are three examples of approaches that have been explored as a way to adapt our current system.

A new phenomenon of plant domestication now dominates human-plant interactions: genetically modified (GM) cultivars. Though GM crops can potentially increase yield, resist herbivory, and provide higher nutrient contents among other benefits, there are significant consequences that must be considered. GM crops can be found throughout the world and as

the trade of monocultures swells, we may be threatening the genetic resources required to develop these transgenic crops in the first place (Daily 1998). Wild genetic resources are important to collect and preserve to ensure genetic security of domesticated plants (Ladizinsky 1998).

Cultures are shaped by the interactions with our surroundings, including use of plants. Ethnobotanical studies, such as some of those discussed in this paper, have greatly contributed to the conservation of biocultural diversity, which is important because we depend on plant communities not only for food but also for construction materials, fuel, medicines, and trade commodities as well as cultural preservation. Zent and Zent (2004) use case studies from tropical environments to showcase the contribution of traditional ecological knowledge (TEK) to the creation and conservation of biodiversity. Human manipulations of their environment can actually increase local biodiversity, acting as "agents of creative disturbance" (Zent & Zent 2004). Furthermore, cultural homogenization is occurring due to the degradation of many ecosystems, threatening the traditional knowledge of many cultures and forcing communities to adopt outside (usually Westernized) medicines, foods, and occupations.

Humanity's success in feeding itself can be assessed based on the proportion of people who have secure access to basic nutritional requirements and the extent to which food production is sustainable. These issues must be treated as localized case-by-case basis, yet globalization encourages standardization of agricultural techniques and leaves limited room for locally appropriate adaptations (Daily et al. 1998). Daily (2001) assesses the "motivation and science behind efforts to characterize and manage ecosystems as capital assets." She has developed an Ecosystem Services Framework as a tool for placing a value on the production of goods, regeneration processes, and stabilization that healthy environments provide for humans. Escalating depletion of our environments threaten the services ecosystems can provide, including endangerment of plant-based products such as food, medicinal plants, and other products.

CONCLUSION

Biogeographic approach to questions of plant domestication helps us identify when and where agricultural first emerged and patterns of domestic evolution and dispersal. Both archaeological and genetic methods contribute to building knowledge of plant domestication. We have seen that scholars still dispute some themes related to the Origin of Agriculture but that overall, plant domestication is a combination of both unintentional and intentional selection by humans, the transition from foraging to farming was gradual with intermediary lifestyles, and

that agriculture emerged primarily as a result of changing climate (i.e. seasonality, warming, precipitation change) at the end of the Pleistocene when domestication became an optimal option of subsistence.

Independent origins of agriculture emerged between 11,000 and 4,000 years ago in the Fertile Crescent, north central Africa, two regions in current day China, Andean South America, Central America and northeast North America. Biogeographical factors explain when and why agriculture emerged in these regions and not others: climate change, seasonality, precipitation changes, physical geography and soil fertility were some of the factors explored in depth in this paper. In addition, we see specific kinds of domesticated species emerge based on the physiological characteristics and requirements of the plants.

Finally, we see the importance of the biogeography of plant domestication in understanding the history and development of agriculture-based societies. Our current economy is primarily based on the production of food through farming but increased consumption pressure and dramatic landscape alterations on top of climate change are beginning to threaten our current lifestyle. Practices such as GMO development, recognizing the importance of biocultural diversity, and integrating ecosystem services are three methods of facing current, problematic trends.

Environmental issues today must be understood in the context of social, political, cultural and economic knowledge. Plant domestication and management in particular must be considered in both ecological and cultural contexts. The study of historical plant evolution under domestication has modern application as we begin an era of significant climactic shifts. Understanding the biogeography of human response to climactic and other environmental changes can better inform political and social decisions today.

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