The Domestication and Migration of Zea mays L. in Association with Holocene Climatic Variance

Kelsey L. Salmon Schreck
The College of Wooster, ksalmonschreck@gmail.com

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The Domestication and Migration of *Zea mays* L. in Association with Holocene Climatic Variance

by

Kelsey Lauren Salmon Schreck

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Abstract

Maize is known to have originated in Mesoamerica from which it spread north and south, adapting to many varied climatic and environmental conditions. This study details the origin of the species *Zea mays* L. The teosinte hypothesis and the concepts of seasonality and scheduling are employed to discuss the domestication of maize by means of human selection. This information is used to highlight the basic circumstances necessary for maize agriculture to be adopted by a human population. Furthermore, climate is examined through the minimum and ideal environmental conditions needed for the successful growth of maize. Environmental cues play a profound role in the phenotypic characteristics a species exhibits; therefore Holocene climactic events are examined in areas with extensive evidence of maize domestication. The minimum requirements for maize growth are compared against the actual conditions during periods of significant climatic change (Little Ice Age, Medieval Warm Period, etc.). Through comparing the ideal versus realized conditions over time, a model for the diffusion of maize from Mesoamerica into North America, with a particular focus on the Southwest and Ohio Valley, is developed.
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"Nature first, then theory. Or, better, Nature and theory closely intertwined while you throw all your intellectual capital at the subject. Love the organisms for themselves first, then strain for general explanations, and, with good fortune, discoveries will follow. If they don't, the love and the pleasure will have been enough."

-E. O. Wilson, from Naturalist (1994)
Chapter I
Introduction

Problem Statement

Maize is cultivated in all regions of the world in a multitude of different environmental and climatic conditions. The crop is so intertwined with past and present culture in the Americas, and now throughout the world, that Walton C. Galinat refers to it as “our symbiotic partner in survival” (Galinat 1992:11). Yet, despite (or perhaps because of) the significance maize holds, the origin of the species continues to be heavily debated. Filling the blanks in the phylogenetic tree of *Zea mays* L. proves to be a complex issue in which individuals from many disciplines (botany, genetics, archaeology, geology, etc.) work together to form and debate hypotheses.

Maize is known to have originated in Mesoamerica, specifically in the Central Balsas region of Mexico (Merrill et al. 2009; Piperno et al. 2007; Piperno and Pearsall 1998; Ranere et al. 2009), from which it spread north and south adapting to many varied climatic and environmental conditions. This study details the origin of the species *Zea mays* L., or maize, using the teosinte hypothesis and the concepts of seasonality and scheduling to discuss the domestication of maize through the process of human selection. This study also examines the environmental and climatic conditions necessary for maize crops to succeed in several regions, as well as the conditions required within a human population for maize agriculture to be adopted.

Furthermore, the domestication of maize as it relates to the transition from Pleistocene to Holocene climate is explored. By comparing the climatic conditions over the course of maize’s spread, a model for the diffusion of maize agriculture from Mesoamerica into North America is developed.
The following research questions are addressed in this study: How did climatic events of the Holocene affect the spread of maize throughout North America? Were changing climatic conditions a factor in the widespread adoption of maize agriculture? Specifically, how did climate contribute to the human transmission and the migration of domesticated maize? Did these climatic changes provide a favorable environment for maize agriculture, or was the adoption of agricultural practices simply a modification in behavior patterns of people during this time period? Furthermore, what, genetically, allows maize to adapt to various regions and climatic conditions throughout the Americas?

The geographic scope of this study follows the transmission of maize agriculture northward from its Mesoamerican center of origin. First examined are climatic changes in early Holocene Mexico, the environment in which maize was domesticated. The scope is then broadened to include initial northward transmission to the American Southwest, finally ending (for the purposes of this study) in the Ohio Valley. Additionally, it should be noted that major climate events do not impact all regions uniformly. Maize was introduced to various regions in different time periods and under various climatic conditions. Thus, the climate events discussed in this study have varying impacts depending on the region being explored.

**Literature Review**

It is the goal of the literature review to situate this study within the greater context of academic writing concerning prehistoric maize domestication. This is done through review of prevailing and supporting hypotheses surrounding the origins of maize through domestication, description of three geographic and cultural centers of maize domestication, and through an overview of climatic variables and episodes of accelerated climate change that may have
influenced crop success. Furthermore, this first chapter serves to highlight the research questions and goals driving this particular study.

**Origins of Maize**

The historic debate surrounding the evolution of maize can be understood through two widely established pieces of evidence, now commonly accepted as fact, and the two critical questions they raise. It is these questions that form the basis for the debate on the evolution of *Zea mays* L.

The first fact, which is referenced in seemingly all scholarly work on maize, is that maize evolved rapidly, likely within 10,000 years from the present (Flannery 1968; Galinat 1992:2; MacNeish and Eubanks 2000:3). Furthermore, shortly (by evolutionary standards) after its divergence, maize dominated the diverse landscapes of Mesoamerica, with hundreds to thousands of landraces known, each presenting countless different phenotypic characteristics (Corral 2008; Galinat 1992:8; Hernández 1985:417; Tian et al. 2009).

The second piece of evidence generally accepted as fact is that modern maize is directly related to a species of teosinte, a wild grass in the *Zea* genus. This means an ancestral teosinte variety, by some biological process (hybridization, mutation, human selection, etc.), gave rise to what would eventual become maize (Corral 2008:1510; Flannery 1973; Galinat 1992:4; Eubanks 2001a; MacNeish and Eubanks 2000:11; Piperno 2014). The fact that there is a relationship between maize and teosinte is never doubted in the literature; rather, it is the process by which this relationship formed that leads scientists to propose and debate new hypotheses.

Despite acknowledging these two lines of evidence, there are two remaining questions, unearthing the answers to which is the critical next step in historic attempts to complete maize’s phylogenetic tree. The questions are: (1) Could a series of sufficient mutations accumulate
rapidly enough within a population of teosinte to give rise to maize, and (2) is it likely that a
landrace of *Tripsacum* and a landrace of teosinte were able to hybridize in the wild, and produce
viable offspring that would eventually give way to early maize? Together these questions form
an either-or debate that has polarized botanists, geneticists, and archaeologists alike. The
following is an overview of the discussion of the origins of maize, as it is presented in the
predominant literature.

*Teosinte Hypothesis*

The teosinte hypothesis for the origin of maize was first proposed by George Beadle in
1939. This hypothesis argues that maize arose from a species of teosinte through the pressures of
human selection for traits beneficial to diet, specifically the trait of four rowed kernels (Eubanks
2001b; Tian et al. 2009; Galinat 1992:4). The teosinte hypothesis favors the possibility that a
series of mutations within the teosinte genome occurred and gave rise to *Zea mays* L. (Beadle

Beadle postulated that mutations at five distinct loci would be enough to successfully
produce offspring with the morphologic qualities of a young maize. The idea that mutations at
just five loci could possibly be responsible for the appearance of maize persists, and is even
supported by chromosomal analysis of the maize genome at specific loci (Tian et. al. 2009:9981).

Further, Beadle’s original hypothesis has consistently been refined since 1939. A specific
annual species of teosinte, *Z. mays* ssp. *parviglumis*, was identified through isozyme analysis and
chloroplast DNA (Doebley 1990) as the most likely extant relative of maize (Corral 2008:1510;
Doebley 1990; Tian et al. 2009:9982). More and more evidence is added to uphold the teosinte
hypothesis as advances are made in chromosomal and DNA analysis.
Tripartite and Tripsacum-diploperennis Hypotheses

The *Tripsacum-diploperennis* hypothesis was proposed by Mangelsdorf and Reeves in 1939 as the tripartite hypothesis for the origin of maize. The tripartite hypothesis assumed maize developed from a, now extinct, wild pod-popcorn maize (Bennetzen et al. 2001:84; Staller 2010). Specifically, it is postulated that the pod-popcorn hybridized with *tripsacum* to produce a modern variety of maize (MacNeish and Eubanks 2000). The hypothesis later morphed into what is known as the *Tripsacum-diploperennis* hypothesis, which states *Zea diploperennis*, a diploid perennial teosinte, crossed with *Tripsacum*, a gammagrass, resulting in annual teosinte. Through backcrossing of this annual teosinte with wild maize, the domesticated form of maize was produced (MacNeish and Eubanks 2000).

The inclusion of the landrace *Z. diploperennis* is the most important development in this hypothesis in recent years. Tripsacum species generally have a haploid chromosome number of n=18, while both maize and teosinte have a haploid number of n=10. Countless *Tripsacum*-teosinte hybrids have been produced in lab settings, but because of their difference in chromosome number these hybrids are sterile. However, MacNeish and Eubanks (2000:13) claim to have produced a fertile *Tripsacum*-teosinte hybrid with maize-like features using *Z. diploperennis*. Moreover, this hypothesis has been tested using restriction fragment length polymorphisms (RFLP) to compare polymorphisms in maize, teosinte, and *Tripsacum* with the hopes of revealing similar polymorphisms indicative of a genetic relationship between the three species (MacNeish and Eubanks 2000). However, the majority of scientific and academic literature published on the origins of maize argues, either explicitly or implicitly, for the validity of the teosinte hypothesis rather than the Tripartite or *Tripsacum-diploperennis* hypothesis.
Range of Habitation

It is postulated by some that maize was first domesticated in the highland regions of Mesoamerica (MacNeish and Eubanks 2000) and from there it spread throughout the Mesoamerican lowlands and into other geographic regions. Alternately, others argue for a lowland origin of maize (Doebley 1990; Piperno 2014; Piperno and Pearsall 1998). Regardless of the specific location of origin, hundreds of landraces appeared by the time of Columbus’ contact with the New World. It is assumed these landraces emerged via basic evolutionary processes that affect populations as a whole, namely “drift, isolation, and adaptation” (Galinat 1992: 8).

However, in the case of maize the impact of human selection cannot be ignored. The preservation of specific landraces for religious and dietary purposes as well as experimental hybridization of races plays a significant role in the genomic structure of maize populations (Galinat 1992; Hernández 1985). It is the symbiotic-like relationship that maize and humans have, which allows for large scale maize cultivation, and makes maize completely dependent upon humans for reproduction (Flannery 1968; Hernández 1985; Galinat 1992).

Additionally, it is essential to consider the role of climate in the domestication of the species. Climate determines the range of characteristics a population of maize or teosinte may express. Thus, the traits available for humans to select for or against in a single species will vary between regions with extremely different climates. The genome of maize exhibits such plasticity of phenotypic expression that, the traits expressed during the conditions of the late Pleistocene or early Holocene may be nothing like those expressed today. This is also true of differential expression of traits between climatic zones and regions later in the Holocene. Thus, it is understood that maize is able to adapt as it enters new zones of habitation, or encounters changes in climate within a region.
Process of Domestication

In order to draw any conclusions on the interactions between maize and human groups one must first understand the processes by which a species is transformed from wild to domesticate. In general, there are four stages leading to the formation of agricultural systems through human manipulation of plant populations. These phases are foraging, cultivation, domestication, and agriculture (Fagan 2000).

The initial stage, foraging, is a behavior regularly exhibited by hunter-gatherer populations. Foraging is the collection of wild foods during natural seasons of growth and within a plant’s known range of habitation. Through this process, humans may accidentally select for traits, but there are no widespread changes to population dynamics (Fagan 2000). Cultivation occurs when populations of plants are intentionally cared for and tended by humans. Examples of behaviors associated with cultivation include weeding, tilling, and transplanting. Each of these actions, by decreasing competition, serves to further the productive life of individual plants or groupings of plants for reasons decided upon by the individual acting.

These behaviors lead to the process of domestication. A plant that is domesticated has been genetically altered in some fundamental way through human selection for traits. Through this process plants become dependent upon humans for their survival and reproduction. The final stage of this process is full-scale agriculture, which refers to intensification in the cultivation, use, and importance of a domesticated species within a population. Agricultural societies alter their landscapes, often dramatically and irreversibly, in order to maximize production of domesticated crops (Fagan 2000).

The above phases represent the process of domestication of a wild plant, leading to agriculture. However, not all cultural groups are the initial domesticators of species that they
cultivate through agricultural practices. The process by which a group adopts crops that were domesticated in another region or by another cultural group is called primary crop acquisition (Minnis 1992).

Many factors contribute to both the process of domestication and the adoption of agriculture within human populations, as well as the plant population being manipulated. For example, climatic conditions impact the rate of transition from domestication to full-scale agriculture within a cultural group. If climate is favorable, the transition will occur rapidly and vice versa. As climate changes, so to does phenotypic expression of traits by a plant species, allowing humans to select for traits best suited to the current environment (Piperno 2014). Furthermore, new stresses on wild food plants could develop, preventing these plants from adequately supporting a group of people. These stresses include an increase in human population or a decrease in plant availability (Minnis 1992). Agriculture can also spread simply because the advantageous outcomes it offers are favored by a population, and they choose, rather than are forced, to adopt agricultural behaviors (Minnis 1992).

Centers of Domestication

Three distinct geographic regions and cultural groups are examined in this paper as centers of maize agriculture. Each represents a separate time period for the initial introduction of maize, and later intensification of maize agriculture. Furthermore, each area is characterized by a distinct climate and regional ecosystem.

The purpose of discussing three geographically separate regions occupied by three culturally distinct societies is to glean a better understanding of the processes by which maize, and agriculture in general, come to dominate the landscape holistically. For the purposes of this study, elements hyper-specific to each culture (burial practices, religious beliefs, iconography,
etc.) are not examined. The cultures themselves are not compared; rather, the response of maize to distinct environments is examined within the framework of human land and plant use strategies. Each culture is examined on a macro scale; fluctuations in diet, interactions with a changing environment, and discernible alteration of settlement patterns and social structure coincident with adoption and intensification of maize-based agriculture are considered.

Specifically, the time of introduction and intensification of maize agriculture are noted for each region. Resulting shifts in social structure as agriculture increases in dominance, and distinct impacts of agricultural practices on local environments are examined. Particular agricultural complexes, and variations in maize characteristic of each area are also contrasted. This is done in the hope of understanding the fluidity and adaptability of maize as a species. Detailed environmental conditions including levels of precipitation, and temperature are discussed within the Data section of this study, in an attempt to understand the basic requirements for maize cultivation.

*Mesoamerica*

The Mexican region of Mesoamerica is maize’s definitive area of origin. However, the specific location within Mexico in which maize first emerged through plant-human interactions is still debated. Material from both the Rio Balsas and Tehuacán areas continuously provide new evidence as some of the earliest locales of maize domestication (Macneish and Eubanks 2000; Macneish 1964). The botanical remains collected from these two areas within Mexico contribute to the formation of a debate on the true location of maize domestication. Those who argue for Tehuacán, or a highland origin of maize, also suggest the teosinte species *Zea mexicana* is the true progenitor of maize (Macneish and Eubanks 2000; Mangelsdorf et al. 1964). While those who support a lowland, or Balsas origin of maize, argue that *Zea mays* ssp. *parviglumis* teosinte
is the variety that gave rise to \( Z. \) mays (Doebley 1990; Piperno and Pearsall 1998; Piperno and Flannery 2000; Piperno et al. 2007).

The Balsas River watershed in the Iguala Valley lies within the modern Guerrerero state of Mexico (Piperno et al. 2007; Ranere et al. 2009). Tehuacán lies near 600 km drive east in the state of Puebla (Figure 1). These earliest forms of maize dating to ca. 4800-3500 B.C. were quite small and minimally beneficial in sustaining human populations (Flannery 1968; Fagan 2000). The potential for maize to succeed improved through time, and can be measured through increases in kernel and cob size, thickness of rachis, and relative resilience to the dramatic fluctuations in temperature and precipitation prevalent in Mesoamerica (Fagan 2000).

Furthermore, maize is the foundation for the Mesoamerican Crop Complex, which consists of corn, beans, squash and chili peppers (Culbert 1978). This combination of plants continues to provide a balanced diet for Mesoamerican peoples, and was the basis for the

![Figure 1. Map indicating relative proximity of Central Balsas Valley and Tehuacán Valley. Both regions have yielded evidence for maize production from the \( Zea \) mays ssp. \( parviglumis \) species of teosinte. (Piperno and Flannery, 2001: 2101, Fig. 1).](image-url)
transition in social structure from small bands of hunter-gatherers to complex hierarchical societies in the Americas.

Southwestern North America

The first maize variety introduced to the Southwest was Chapalote at ca. 3000 BP in the Archaic period (Fish and Fish 1994). However, Chapalote maize was not well suited to the conditions of the arid Southwest. During the Archaic, the climate of the southwestern United States was relatively stable, but rainfall was sporadic. Under these conditions cultivation and agriculture were advantageous behaviors compared to hunting and gathering. With such variable rainfall, wild populations of plants were unpredictable in frequency and geographic spread (Fagan 2000).

However, it was not until the extremely productive and environmentally well suited Maiz de Ocho variety was introduced to the Southwest that maize agriculture took hold (ca. 800 B.C.) (Fish and Fish 1994). This eight-rowed maize was a staple of the Upper Sonoran Agricultural Complex along with beans and squash. Additionally, Maiz de Ocho served as the basis for the full scale agricultural systems exhibited by the Hohokam and later cultural groups (Fish and Fish 1994).

Ohio Valley

The introduction of maize agriculture to the Ohio Valley proves to be unique in many ways, predominantly due to the presence of native domesticates and agricultural behaviors in the region preceding the appearance of maize. Prior to the explosion of maize-based agriculture in the Ohio Valley, the Eastern Agricultural Complex (EAC) dominated. Plants such as chenopod, sunflower, maygrass, knotweed, sumpweed, and cucurbits, constituted the EAC before the integration of maize (Greenlee 2006).
Maize was introduced to the region as early as 170 B.C.-A.D. 60 as evidenced by remains from the Holding site (Fagan 2000; Fritz 1993). Maize from this period is generally the eight-rowed Maiz de Ocho from the southwestern United States (Fagan 2000). Maize remained a minor crop until ca. A.D. 800-900, when it increased in frequency in the archaeological record (Fritz 1993; Greenlee 2006).

By A.D. 900-1000 the eight-rowed Northern Flint variety of maize emerged. Adapted to northern climate and growing conditions due to its earlier flowering time, it rapidly dominated the landscape (Smith 1989). This is coincident with the Fort Ancient cultural phase (ca. A.D. 1000-1800) in which wild plants and native domesticates were all but abandoned. Domesticated species exploited during this phase include the classic triad of corn, beans, and squash, as well as chenopods (Rossen 1992).

All three regions are characterized by a period of time between the introduction of maize to the region, and its eventual domination of the landscape. This lag is recognized as a period of transition and adaptation within the species. During this interval, maize populations evolve through expression of new traits, making the plant better suited to the environmental conditions specific to the new region (Fagan 2000; Fish and Fish 1994; Fritz 1993).

Climate

On the geologic time scale the transition from foraging to agriculture-based societies closely corresponds with the shift from Pleistocene to Holocene climate (Brooke 2014; Hetherington and Reid 2010; Marceau and Myers 2006; Mayewski et al. 2004; Piperno 2006, 2014). The connection between climate and regional development of agriculture is explored in this study. However, it is important to note that a perceived correlation between shifts in climatic periods and changes in agricultural systems in no way proves a causal relationship. I do not
argue for environmental determinism. Instead, I highlight interactions between humans and the resources available within their environment, which, at any given point in time are plentiful or poor depending upon overarching climatic conditions.

The Holocene began roughly 11,500 cal years BP (Mayewski et al. 2004). As glaciers that dominated the Pleistocene landscape retreated northward, so too did glacial conditions and ecosystems. The last glacial maximum ended around 14,600 BP, and was followed by a postglacial interval of alternately cold and warm periods. The end of this interval signaled an overall shift in global climate toward Holocene conditions (Brooke 2014).

The mechanisms behind changes in climate are multifold. Factors such as the precession, eccentricity, and obliquity of the Earth; circulation patterns in the atmosphere and oceans; the amount of energy going into and out of the Earth’s atmosphere. These are just a few examples of the interconnected components of the Earth’s climate system that impact the conditions experienced by plants and animals residing on the Earth’s surface. The harmony and synchronism of all these elements allow for balance in the Earth’s climate system. If one component is perturbed, a ripple is sent though the entire system, resulting in widespread change. Thus, the mechanisms behind climate change, and stasis, can be viewed as one and the same. At certain points in time environmental changes are a part of the overarching cycling of events; at other times they are indicators of a flux in the system (Hetherington and Reid 2010).

Despite the retreat of Pleistocene glaciers, the Holocene has not been without climatic variability. There have been many periods of abrupt climate change since the onset of the Holocene period. These abrupt shifts in climate, as their name suggests, are significant changes in global climate that arise over the course of a very short period of time. However, the effects of abrupt climate changes (ACC) can persist for several hundred to a few thousand years. These
events represent fluctuations in environmental conditions with significant implications for human populations and ecosystems throughout the world (Mayewski et al. 2004).

For the purposes of this study, the events examined are the Younger Dryas, the 5.1 ka event, the Medieval Climatic Anomaly, and the Little Ice Age. Each of the aforementioned events are examined briefly in this chapter, but are explored in greater detail and in relation to maize domestication in a subsequent chapter.

Younger Dryas

In the period 12,000 BP – 10,000 BP, significant environmental change took place across globally as the transition from Pleistocene to Holocene conditions took place. Atmospheric carbon dioxide levels increased (c. 265-270 ppmv) to around one third higher than during previous, glacial, periods. Precipitation also intensified by a factor of 20-40%, and temperatures rose by nearly 6°C (Piperno 2014). These conditions, which prove to be distinct from both Pleistocene and modern episodes, allowed for the development of a unique environment on Earth. Specifically, one that encouraged altered interactions between people and plants due to the expression of novel traits within plant populations (Piperno 2014). During this period, at about 11,500 BP a glacial termination event referred to as the Younger Dryas (YD) began. The YD is an early Holocene period characterized by low temperatures and low precipitation (Brooke 2014; Hetherington and Reid 2010). It is often suggested that the cool and dry conditions around and during the time of the YD provided an environment uniquely suited to early domestication of plants (Brooke 2014; Hetherington and Reid 2010; Piperno 2014).

6000-5000 BP Interval, and 5.1ka Aridization

Climate changes in the 6000-5000 BP interval were likely triggered by a decline in incoming solar radiation (insolation) (Mayowski et al. 2004). This is seen as the cause of an
increase in aridity and variability in precipitation across the middle latitudes (Mayowski et al. 2004; Drake et al. 2012). The effects of this shift in climate are particularly evident through the 5.1 ka aridification across the American Southwest. This period is denoted by a transition from ponderosa forests to piñon-juniper woodlands in the Southwest (Drake et al. 2012). As this biome shift occurred, cultivation and food storage patterns developed within Southwestern populations (Drake et al. 2012). Furthermore, the presence of these behaviors was essential to the adoption of maize by populations in the American Southwest.

**Medieval Climate Anomaly**

The Medieval Climate Anomaly (MCA), also refereed to as the Medieval Climate Optimum and the Medieval Warm period, was an extended period of climatic change occurring roughly from A.D. 900-1275 (Brooke 2014). This change in climate is believed to have been forced by a combination of global climatic phenomena. These include decreased volcanism throughout the world, which lead to to lower levels of dark ash particulates in the atmosphere. Ultimately, causing an increase in the amount of solar radiation allowed into the Earth’s atmosphere (Brooke 2014; Mann, et al. 2009). This high solar irradiance caused generally warmer global temperatures on Earth. Furthermore, the MCA is denoted by La Niña conditions in the west, and intensified thermohaline circulation patterns, which caused drought in tropical zones (Brooke 2014).

**Little Ice Age**
Another serious climatic event, the Little Ice Age, occurred at the closing of the Medieval Climate Anomaly, around A.D. 1300-1870. Climate of the Little Ice Age (LIA) is characterized by El Niño conditions, cold winters and cold summers throughout the world. This period was brought about by a series of solar minimums and an increase in global volcanism (Brooke 2014). The consistently cold weather of the LIA seriously impacted crop growth, as growing seasons were shortened tremendously.

A Note on Dates

Extreme caution must be taken in proper recording of dates when conducting a study such as this, which crosses repeatedly back and forth between events recorded on the geologic time scale and events within several cultural chronologies. As the data within this study were collected mainly through a process of literature review, they are subject to the constraints of their original collection and publication. A few papers examined for this study were written prior to the development of radiocarbon dating, while other papers make use of the highly accurate Accelerator Mass Spectrometry (AMS) dating process. Because of this range in techniques used to produce dates, and the interdisciplinary nature of examining climatic events in a cultural context, readers will find that dates within this paper appear in A.D./B.C., BP, and cal BP format. It is important also to note that dates that appear throughout the text remain in the format of their original publication.

The story of maize is unique; its components are numerous, and cross the boundaries of multiple academic fields. This study bridges the gap between archaeological, geological, and genetic studies relating to the varied history of maize domestication. The articles and hypotheses detailed within this chapter are evaluated in an effort to understand the interplay between climate, plants and people. Special attention is paid to the ability individuals have to affect the
speciation of maize and regulate the cultural changes that fundamentally follow a widespread transition to agriculture.
Chapter II
Theory

This chapter reviews four theories often applied when examining social change. Drawing on the reviewed theories, the chapter then outlines a model for the interplay between climatic, regional, and human forcings on the domestication of maize and the adoption of maize agriculture by a culture. Ultimately, this model is situated within the framework of the teosinte hypothesis for the divergence of maize as a domesticated species, and is applied to the migration and adoption of maize in a variety of regions in an effort to explain its persistence as a species.

The aim of the theory chapter is to situate the research questions specific to this paper within a theoretical framework, in the form of a model, that has broader applications. The specific research questions to be addressed are: (1) how did domesticated maize diverge as a genetically and morphologically unique species from teosinte within Mesoamerica? (2) What roles did humans and climate play in the emergence of domesticated maize and its spread northward? (3) To what extent has maize morphology changed over the course of its history as a species and what pressures can these morphologic changes be attributed to? (4) How did social structure within human populations change as maize was introduced and eventually became a staple food?

Also, it is important to note that when examining the origins of agriculture and domestication of a species often, one must either accept a slow and gradual Darwinian evolution via natural selection, or one must accept a rapid punctuated equilibrium consisting of periods of evolution and stasis. Each of the theories outlined below as well as each of the hypotheses for the domestication of maize must follow one of these assumptions on the rate of evolution. Generally, it is understood that maize evolved rapidly with the aid of climate change and human selection.
Coevolution

David Rindos is well known for his theory on the origins of agriculture through “coevolution”. In this approach agriculture is developed and adopted through a gradual process, thus it best fits within the framework of evolution via natural selection. In Rindos’ model, agriculture is defined as “the outgrowth of evolutionary potentials which may develop whenever an animal consistently feeds upon any set of food plants” (Rindos 1980: 751). Rindos stresses the interdependency of the consumer and the consumed, explaining that the two evolve together, co-dependent upon each other. In Rindos’ coevolutionary theory humans and plants exist in a symbiotic relationship with one another (Rindos 1980: 752).

The main body of evidence for Rindos’ argument comes from what he calls “nonhuman agricultural systems” (Rindos 1980: 753). Most importantly, he uses the example of fire ants and their symbiosis with a species of woody plant, which they protect from predators in order to use the plant as a resource. Rindos (1980: 755) also stresses that nonhuman selection pressures are omnipresent within all ecological systems, and thus are actors in shaping human agricultural systems.

Within coevolution, Rindos assumes that there are greater overarching selective pressures at play than those of human selection. This theory is successful in that it shows human populations are subject to the selective pressures of their environment. However, Rindos’ theory branches into evolutionary determinism in which all animal organisms are subject to symbiotic relationships with plants. In that sense, neither party involved actively makes meaningful decisions; instead each unwittingly takes and is taken advantage of in order to survive. For example, an increase in abundance of maize brought on by the transition to an agricultural production system benefits humans and maize equally as species; the carrying capacity of the
land is increased so as to support more human life, and more maize is able to survive and reproduce as humans continually plant and harvest it (Rindos 1980: 763).

While Rindos’ argument is unique, and it is true that domestication of maize favors both humans and maize from an evolutionary standpoint, his argument anthropomorphizes the plant within the symbiotic relationship, allowing it just as much station in the development of that relationship as humans. In regards to domestication and the development of agriculture, it is fair to allow humans more agency than Rindos’ coevolution does.

**Systems Theory**

Systems theory involves many components that come together to form a succinct argument for the operation of a system, defined as the functional combination of human and environment. These two pieces influence one another both directly and indirectly, causing them to converge and form a web of interconnections.

The first aspect of systems theory, as discussed by Flannery (1968), is cybernetics. Cybernetics involve a system of relationships (causes and reactions) required for the flow of information within a system. The two main components of cybernetics are negative feedback and positive feedback. The former acts to prevent deviation from equilibrium, or promotes stability within a system. While the latter amplifies deviations from equilibrium, causing equilibrium to be achieved at a “higher” level than it was previously (Flannery 1968). Both types of feedback are part of procurement systems in which humans utilize resources within an ecosystem to ensure survival.

Next in Flannery’s systems theory are the mechanisms of regulation, namely seasonality and scheduling. Together these mechanisms form a “deviation-counteracting feedback system”
(Flannery 1968:79). They are aids in maintaining equilibrium at its current position in time and place.

Seasonality, as it sounds, is a reference to the availability of resources in an area at a given point in time or season. It is the relative abundance or scarcity of usable resources within an ecosystem, and is dictated by external pressures. On the other hand, humans and cultural pressures originating from within a system determine scheduling, or the patterns of collecting and harvesting of plants by humans within a season (Flannery 1968).

The processes of seasonality and scheduling work together, unless a pressure forces one to change. When enough changes build up within a system of scheduling, then a “deviation-amplifying process” occurs and causes positive feedback within the system, meaning the equilibrium of a system is forced to shift from its original state. Flannery argues that these “deviation-amplifying processes” are the driving force behind cultural change. He uses adoption of a sedentary system of agriculture over that of a hunter-gatherer system as an example of such a deviation from previous equilibrium. In this example, the system deviated from gathering because of human reactions to seasonality (i.e. changes in scheduling), and then amplified because of the increased potential for production and storage within an agricultural system (Flannery 1968).

In essence, Flannery argues that one should not look for the singular exceptions in the archaeological record; instead one should look at shifts in overarching patterns, as these will best indicate how cultural groups changed over time (Flannery 1968). Thus, Flannery stresses the importance of the group as a whole entity rather than the significance of the decisions of individual actors within the system.
**Resilience Theory**

Questions regarding the source of change within a system are the main queries of resilience theory. In order to understand these, resilience theory examines links between dynamic cultural and ecological cycles across space and throughout time.

A main component of resilience theory is its diagrammatic representation of an adaptive cycle as a figure eight (Figure 2). Each adaptive cycle represents a population’s strategies for land use and subsistence in a setting at a given point in time. As strategies change due to external or internal pressures, a new adaptive cycle develops, and thus there is a transition from one figure eight to another. This dynamism is represented in the nesting of present and past adaptive cycles, forming a hierarchy of figure eights. A new cycle will always be situated in the framework of the old. Redman et al. (2009) suggest that nesting aids in stabilizing a society after change occurs, as it serves to remind present societies of past strategies. However, if too many
connections are made between nesting hierarchies, a society will destabilize, indicating lack of resilience due to over complexity (Redman et al. 2009).

According to resilience theory, after destabilization comes a period of reorganization in which a new adaptive cycle is formed and the process begins anew. This appears to provide a model for applying punctuated equilibrium to cultural change. Resilience theory, like punctuated equilibrium, stresses that systems transition between periods of stability and periods of change. However, in resilience theory, neither period is considered to be equilibrium (Redman et al. 2009). Instead, resilience theory considers multiple equilibria to be possible within a single ecosystem.

Thus, the main factor impacting social change is the interplay between destabilizing forces, which increase opportunity and diversity, and stabilizing forces, which increase productivity and social memory (Redman et al. 2009). Systems are resilient if they can absorb disturbances, meaning, dynamic systems are more resilient and long lasting. On the other hand, systems that are static break down in response to perturbation. Furthermore, as periods of stasis and periods of change are both expected to occur within the framework of an adaptive cycle, changes to a system are not always viewed as detrimental. Rather, they are influenced by “particular dynamics, conditions, and opportunities” within a system and may contribute to the formation of a new adaptive cycle, or simply to alteration of the current cycle (Redman et al. 2009: 25).

While resilience theory has many similarities to systems theory, there are a few key differences. Namely, societies even when operating under a completely novel adaptive cycle have the ability to remember past cycles and learn from them. Redman et al. (2009) stress that this social memory is key to building a resilient adaptive cycle; in such a system, past mistakes
would not be repeated. Also, resilience theory stresses that the scale of a society, both spatial and temporal, influences the characteristics of their adaptive cycles (Redman et al. 2009).

**Agency Theory**

When applied to archaeology, agency theory is derived from reactions to processual archaeological theories such as Flannery’s systems approach. Whereas processual archaeologists argue for the significance of the group in constructing social change, postprocessualists argue for the importance of individual thought and action within a system.

Ian Hodder presents the importance of active participation of individuals within a society by arguing that the past is meaningfully constituted. In other words, individuals naturally react to the system around them; they make the choice to react with or against the status quo or equilibrium of their society (Hodder 1985). These reactions are evidenced through periods of stasis or periods of change within the archaeological record. In this sense, Hodder’s postprocessualism argues that individuals are not “duped” by the machine, or the overarching sociopolitical system. Instead, they have the ability to act against it and may choose to do so or not (Hodder 1985). Thus, in recognizing the action of individuals one does not reject acknowledgment of group action, but instead one allows for the possibility of deviance from the group goals as individuals act on features of the environment surrounding them (Hodder 1986).

**Model**

After reviewing the preceding theories, a few questions remain regarding domestication and cultural shifts toward agricultural production. These questions guide the following model. Specifically, these questions fall into two categories, (1) How do humans impact their environment, and (2) How does climate impact local populations of plants and animals, (including humans).
First addressed is the magnitude of the impact of climate on human populations. This can be explained through understanding that humans are inherently a part of the ecological system they are situated within. This extends to the impacts of global scale climate forcings. Yet, climatic variability is often overlooked in systems attempting to explain social change. Climate is discounted for the same reason it is of primary importance; global climate and the various components that force it to change are the overarching, often unseen, macro level mechanisms by which ecosystems change. Because it is of such large-scale climate is unseen, and because it is unseen it is ignored. However, climatic fluctuations are of the utmost importance in shaping the environments in which people live. In this sense, climate (macro scale) dictates the range of plants and the phenotypic characteristics available for humans to act on within a population (micro scale) at a given point in time. Theories attempting to explain social change can often focus solely on the micro scale human or population variation, and forget about the overarching, macro, climatic variation that dictates availability of resources within an ecosystem. They focus on human expression of culture and how it changes within that culture, rather than examining external influences that contribute to these shifts in cultural paradigms. This conflict raises the question, is the cause of culture change or the culture change itself of greater importance? In the end, understanding both the internal and external deviations is necessary to comprehend events of the past. Incorporating micro scale actions and climate into a model helps to accommodate the element of individual agency within a system.

Interactions between climate, ecosystems, and human adaptation form the basis for explaining how cultures change over time, specifically in regard to shifts in subsistence strategies toward agriculture. Each smaller cycle (climate, ecosystem, and human) is characterized by
dynamic interactions within. These cycles also interact with one another forming a larger scale system for social and environmental change (Figure 3).

Figure 3. Model for interactions between global climate forcings, regional ecosystem variation, and cultural adaptations. Straight arrows show interplay between aspects of the larger system. Interactions within each smaller dynamic system are represented by curved arrows. (After Dearing 2006: 598, Fig. 1).

In considering small-scale cycles within a larger system of interactions, the adaptation of maize to local ecosystems after being introduced may be explained; this application of the model is explored in the Data chapter of this study.

Next, the questions of human impacts on their environment are considered. These include: what are the consequences of human action on the environment, and to what extent do individuals or groups adapt to their environment? Also, what is the role of the individual actor in
the domestication of species and how do individuals play into the functions of an ecosystem? Through understanding these cultural, human-environment interactions one can better understand the process by which species are domesticated and agriculture is adopted.

It is undeniable that people are influenced by the environment in which they live. A systematic approach to social change stresses the uniformity of this influence. In this sense, a web of definable systems exists which governs human actions leading to social change within the boundaries of such a system. Change that deviates drastically from one system is just a transition to another, equally definable system through an increase in the resilience of the prior system or a shift to an entirely new one.

However, when examining the transition of a cultural group between two entirely different subsistence strategies, different concerns are raised than those of simpler social changes. Such is the case for study of the transition from a hunter-gatherer social structure to an agricultural society. More complicated still is the riddle of the precursor to agriculture, the cultivation and eventual domestication of a given species. To examine domestication with only a systems approach is to deny the influence of any individual decision and action within that system.

Manipulation of a species to the point of domestication can be viewed as a change to the environment that humans exist within, which leads to astounding social change. Large-scale cultural and social paradigm shifts generally begin through small-scale, grassroots efforts by a small number of individuals. Through incorporating this idea into a traditional systems approach, like those of Flannery and Redman, the importance of the thought processes and actions of individuals operating within the context of a larger system is considered. As mentioned above, humans are inextricably linked to their environment, but in examining the origins of agriculture
the question arises, can you apply the same theories to social and environmental change?

Furthermore, can these social theories be adapted to incorporate both the environmental and social changes associated with a transition to agriculture?

It is impossible to deny that groups and individual people directly influence their environment and vice-versa. However, this is not the deterministic coevolution of Rindos (1980), but rather a relationship in which humans make conscious decisions to use and thus manipulate plant life. This, in turn, causes mutually beneficial relationships to develop between plant and animal (including human) populations. These relationships stay the same or change depending on external pressures to the system, namely climate, and internal pressures like overuse and population growth (i.e., deviation from equilibrium).

Furthermore, if a system is viewed as an ecosystem with human inhabitants, then the actions of individuals cannot be ignored for the sake of the function of the system as a whole; systems do not function separate from individuals. Instead, individuals play a key role in influencing a system through making decisions in reaction to their environment, as stated above. This leads to deviation from the previous organization within a system. Individual actions, deviating from or amplifying a cultural paradigm, and the inevitable resulting actions of the group are the mechanisms that drive social change. In turn these elements can cause environmental change within the system.

These roles and relationships between humans and their environment can be seen as a circular system wherein each single element influences most directly the element immediately following it in a clockwise direction (Figure 4).

These relationships follow a logical order starting from the largest scale, the environment that directly impacts seasonality through weather conditions. This in turn is responsible for the
relative abundance or scarcity of resources within an ecosystem. Then, humans come into play as they must harvest or collect based on that relative abundance, leading to the development of scheduling patterns. Eventually, human pressures on the ecosystem (such as population growth, or overuse of a resource) create an imbalance requiring a shift in the system. This allows for a change in the carrying capacity of the land and/or change in human use of available resources.

Furthermore, the model can be examined through groupings of relationships. The relationships on the left half of the circle are short-term. They are the ephemeral interactions of human use of the resources available within their ecosystem at a given point in time. On the
other hand, the right side of the chart dictates the more unpredictable availability of these resources. The right side relationships are indicative of the influence of climate on ecosystems and thus availability of resources. These take longer to form and last longer than those on the left side, but are more easily achieved than the top and bottom interactions.

The most complex relationship explained within this framework is the interaction between the top and the bottom of the chart. These are the long-term impacts of humans on their environment and the long-term affects of the environment on society as a whole and the shaping of cultural paradigms. The most obvious example of this connection is that of the modern impact humans have on global climate change, or anthropogenic climate change. These relationships are beginning to be clarified through modern research, and they prove to be the largest scale and the most impactful of any of the interconnections.

The interactions between the top and bottom elements can be understood as a feedback loop between environment and humans. If the feedback is positive, then change would be amplified and large-scale deviations from the previous equilibrium occur. On the other hand, the presence of negative feedback represents resilience of a system, and the previous equilibrium will be maintained.

Forces that cause deviations from or maintenance of a certain equilibrium represent the risk inherent within subsistence systems. Mitigation of this subsistence risk is possible through active decision-making processes of individuals by means of diversification and intensification of a subsistence strategy (Martson 2011). Transitioning from foraging to agricultural practices does not guarantee abundance of resources; domesticated species are just as subject to variation in the environment as wild types. However, domestication and complex agricultural practices
(terracing, irrigation, etc.) offer increased predictability of crop yields (Barker 2006). Thus agriculture allows for ease of scheduling by human populations.

The initial adoption of agriculture presents an addition of risk in the subsistence strategy of a cultural group. In the American Southwest this risk is due to variable levels of precipitation from season to season. Wild foods in this region tend to be xerophytic, and thus aren’t susceptible to the pressures of variable precipitation levels. However, an intensification of cultivation practices within a culture often leads to increasing dependence on a few plant species. This dependency on cultivated plants is a half-way-point to an agricultural system. For human populations, agriculture, generally, from year to year represents a higher level of control over timing and growth of plants needed for sustenance. Furthermore, agricultural systems allow individuals to select the area that they cultivate, thus they are able to grow crops in fertile areas, further minimizing the risk, and maximizing control (Minnis 1992). This opportunity to control aspects of crop growth often outweighs the risk of crop failure inherent in variable climatic zones, and helps to explain the frequency with which cultural groups transitioned to agricultural systems in antiquity.

Applied to the teosinte hypothesis, the theoretical model above informs the argument that maize evolved via human selective pressures from a landrace of teosinte. Evidence for this hypothesis can be seen simply in the number of chromosomes, ten, which teosinte and maize both have. However, even more specifically, the pressures of human selection on the evolution of maize can be seen through the lack of any brittle cobbled remains of maize in the archaeological record. If corn never had a stage with a brittle cob, then individual corn seeds must always have been dispersed by human action since a strong cob prevents dehiscence of corn kernels from the cob (Beadle 1980). Furthermore, the divergence of maize from a species of
teosinte was made possible by the change in climatic conditions at the onset of the Holocene. All together, when the evidence is examined through a modified systems theory that emphasizes the importance of individual actors, a compelling argument for the teosinte hypothesis is made, and human use of maize agriculture can be understood in relation to changing climate.
Chapter III
Methods

The data considered in this study were collected through a process of literature review. Sources were gathered from online databases, as well as through the College of Wooster library, InterLibrary Loan (ILLiad), and Colleges of Ohio Networked System Online for Research and Teaching (CONSORT) systems. The primary databases employed in this study were JSTOR and EBSCOhost’s Academic Search Complete. Searches from these databases yielded mainly articles from journals including, but not limited to, Economic Botany, Latin American Antiquity, Kiva, Annual Review of Anthropology, Anthropological Archaeology, Current Anthropology, Proceedings of the National Academy of Sciences (PNAS), and Quaternary Research.

Through preliminary research, the topic of this study was narrowed and refined. Then articles and books were examined in great depth for information pertinent to the topic. Information was collected from articles in phases, just as this study was written in phases. After a significant amount of information was collected and enough of the prominent theory surrounding the topic was reviewed, a model was developed and used to analyze the data collected through research. Conclusions of this study were drawn through application of a distinct model to a set of data built from preexisting research. The theoretical framework applied to the data set was influenced by several main theorists and constitutes a modified form of both resilience and systems theories. Information deduced from application of the theoretical framework is novel, but is supported by findings of previous researchers.

A grant from the College of Wooster’s Copeland Fund for Independent Study made it possible for me to attend a seminar in paleoethnobotany during July 2014 in Riley, Oregon. Within this field study associated with the Rimrock Draw Rockshelter, I was exposed to all
phases of macrobotanical analysis. I aided in the extraction of sediment samples from hearth deposits and then performed floatation of these samples. I also analyzed samples under a microscope, sorting seeds from sediment, painstakingly attempting to identify and record each seed and seed fragment extracted. In addition to examining seeds, I collected charcoal and attempted to identify the plant of origin based on the cross-sectional pore structure of charred wood fragments.

This seminar provided me with the basic background in paleoethnobotanical methods necessary to fully comprehend site reports and other papers used within this study. I learned the methods used throughout the world to examine botanical remains from an archaeological context. Additionally, as the Rimrock Draw Rockshelter site was occupied by non-agriculturalists, I was exposed to ways in which the manipulation and collection of wild plants, in contrast to domesticated plants, may be evident in the archaeological record. Furthermore, examining botanical remains from several different occupational phases allowed me to understand how archaeological plant material aids in reconstructing prehistoric environments. Specifically, how changes in flora in a single location throughout time can be used to indicate changes in environment.
Chapter IV
Data

Maize agriculture is now ubiquitous throughout the Americas. However, the species that
gave rise to maize, teosinte, is not currently and has never been present in all of the Americas.
For this reason, objectives behind the study of maize domestication are expansive and often vary
between disciplines, as the history of maize cultivation applies, not only to reconstructing past
life-ways, but also to concerns of the future genetic diversity of a now world-wide staple crop.
Reconstructing the origins and beginnings of maize are key to understanding and even designing
the future of the species.

Mesoamerica is widely accepted to be the center of origin of maize agriculture,
specifically, in the Central Balsas Region of Mexico (Merrill et al. 2009; Piperno 2014; Piperno
mays* ssp. *parviglumis* a species of annual teosinte, can be found in this region. Another area of
interest to the origins of maize is the Tehuácan Valley, where some of the oldest examples of
maize exploitation by humans have been excavated. Macneish (1964) and others originally
proposed the Mesoamerican highland region of the Tehuácan Valley to be the origin place of
maize (Macneish and Eubanks 2000), but more recent research supports a Rio Balsas, or lowland
origin (Merrill et al. 2009; Piperno 2014; Piperno et al. 2007; Piperno and Pearsall 1998; Ranere
et al. 2009). The divide between the lowland and highland hypotheses tends to fall along the
lines of the teosinte and tripsacum hypotheses for the origins of maize, with those who advocate
for the teosinte hypothesis also supporting a lowland origin, and vice versa. Although this study
argues for the teosinte hypothesis, sites within the Tehuácan Valley are discussed at length
within this chapter. The teosinte hypothesis tends to be supported, overwhelmingly, by modern
genetic and climatological experiments. However, occupational phases are better documented in the literature regarding the Tehuácan Valley. For that reason, data from both regions are used in this study to discuss maize origins.

Furthermore, the transfer of locally developed agricultural skills and technology from the Mesoamerican center of origin, through the 'desert borderlands', and into North America proves to be just as controversial a topic as the long debate surrounding the origins of maize (Mangelsdorf et al. 1964; Minnis 1992). The diffusion of maize into North America highlights the ability of maize to adapt to multiple environmental conditions. It also provides pertinent examples of a transition to an agricultural system among different cultures and landscapes.

This study examines botanical remains from sites occupied by groups of maize agriculturalists so as to denote key changes in maize morphology between the three geographically and chronologically separate adoptions of maize agriculture. Research specifically focuses on sites in the Tehuacán Valley in Mesoamerica, regarded to be one of the oldest locations of maize cultivation and domestication (Mangelsdorf et al. 1964; MacNeish 1946). Furthermore, agricultural developments in the Sonoran Desert, an area of the American Southwest, long occupied by the Hohokam are studied. Finally, I explore the transition from a native crop complex to the Eastern Agricultural Complex, a maize-based subsistence system in the Ohio Valley. By examining these areas in conjunction, I hope to gain an understanding of the origins of maize agriculture, and the evolutionary distinctions in the species that developed in separate environments. By studying evidence of agriculture excavated at each of these sites, a better understanding may be gained of the human tendency toward cultivation practices leading to domestication of a species.
Much can be said specifically, about how the transition to sedentism and adoption of full-scale maize agriculture impacted human groups. Rather than incorporating much of the literature on alterations to social structure in regards to hierarchical arrangement, ceremonial practices, and human health, etc., this paper focuses mainly on the evolution of maize over time and space. Evidence for this process is drawn from morphologic and genetic analysis of plant remains excavated from various archaeological contexts. Thus, this study focuses on the plant materials themselves and how they change; it references overarching changes in social structure of groups as those groups transition to sedentary agricultural societies, as these transitions relate to coinciding changes in maize morphology. This study of changes in morphology over time is overlaid by an examination of changing climate.

To enhance the information on regional adoption of cultivation and domestication of maize, evidence for the transition from teosinte to maize is explored. This includes both the genotypic and phenotypic data that contribute to the teosinte hypothesis for the domestication of maize.

This chapter presents data collected in the field and lab, taken from publications by leading scholars. These data were collected in the Tehuacán Valley, Hohokam settlements in the American Southwest, and the Ohio Valley.

**Genetic Foundations for Maize Adaptability**

*Beadle’s Hypothesis for the Domestication of Maize*

It has long been suggested by George Beadle (1980) that the transition from teosinte to maize could have occurred through adaptations to four or five major genes. Beadle originally proposed this hypothesis after completing research on teosinte that made use of Mendelian genetic principles, and physical crosses of live plants. Evidence collected through modern
genetic analysis continues to support the idea that teosinte is the precursor to modern maize (Galinat 1974, 1992; Tian et al. 2009). However, recently further developments within the field of genetics caused the simplicity of the mechanism proposed by Beadle to be called into question (Wallace et al. 2014).

Beadle’s hypothesis found much support through modern research. In particular, the technique of Quantitative Trait Loci (QTL) analysis is being used to examine differences at specific loci within the teosinte and maize genomes (Tian et al. 2009). Through QTL analysis five major loci have been identified that could be responsible for the emergence of maize.

The first gene altered was for glumes or leaf-like bracts around individual grains (Galinat 1992; Tian et al. 2009). Glume formation is controlled by the gene teosinte glume architecture 1 (tga1) on chromosome four of teosinte (Tian et al. 2009). The first step in the transition from teosinte to maize was selection against tga1, and the formation of tough glumed seeds. This slowly gave way to the soft kernels of modern maize.

Another trait that distinguishes teosinte from maize is the number of rows or ranks of seeds contained on an individual spike of a mature plant. This transition from the single rank of a teosinte spike to the multiple rows of a maize cob is a complex, multi-step process. First the kernel pedicle or rachis must stiffen, and the inflorescence must transition to a pistillate form (Galinat 1974, 1992). Following this change in pedicle morphology the kernels compress together, allowing for the formation of multiple ranks and cob structure (Galinat 1974, 1992). Furthermore, the formation of cob structure along with the stiffening of the rachis prevent cob disarticulation (Galinat 1974). Thus, the non-shattering cob of maize and the complete dependence of the species on humans for seed dispersal formed (Galinat 1992).
The final trait selected for, leading to the formation of maize from teosinte, is in the architecture of the plant as a whole. Maize exhibits a branching architecture with large female cobs close to a central stock. Alternatively, teosinte plants present male tassels or seed spikes which terminate long branches. This morphological change occurred through disarticulation of the *teosinte branched 1* (*tb1*) gene (Tian et al. 2009).

According to Beadle, after this sequence of changes the divergence of maize from the teosinte lineage was complete. From this original form the species radiated, adapting to innumerable environs. Over time, cobs developed greater numbers and larger kernels to meet the demands of human selection pressures.

Current research indicates that the domestication of maize, rather than resulting from changes to four or five major genes, was actually the result of thousands of closely linked genes affecting a few major traits (Wallace et al. 2014). These groupings of genes were responsible for the changes observed by Beadle.

*Domestication in an Early Holocene Context*

Many researchers have linked the emergence of domesticated crops to the transition from Pleistocene to Holocene conditions (Brooke 2014; Piperno 2014). These dramatic domestication events are exemplified around the time frame of the Younger Dryas, a glacial termination event (ca. 11,500 BP), which signaled the end of the Pleistocene period. The near one-third increase in carbon dioxide levels during this period, in comparison to Pleistocene conditions, along with intensification of precipitation by a factor of 20-40%, likely allowed for increased rates of photosynthesis and efficiency in water use by plants (Piperno 2014). In turn, these conditions caused unique expression of traits in plant populations, like Mesoamerican teosinte species. These factors likely encouraged hunter-gatherer groups to cultivate wild plants. (Piperno 2014).
Genetic Diversity Post-Domestication

Following the process of domestication, diversity within the maize genome was bottlenecked, allowing only a certain amount of the variation in the teosinte genome to be transmitted. However, as cultural groups throughout the Americas adopted maize agriculture, the species was exposed to novel selection pressures via diffusion into new environments (Figure 5). This resulted in the development and expression of countless unique phenotypes (Wallace et al. 2014).

Figure 5. Maize migrated from the Balsas river valley to the rest of the Americas, occupying a vast range of topographic and ecological niches. Hypothesized migratory path of maize from Mesoamerica is depicted with arrows. (Wallace et al. 2014: 34, fig. 2).

Maize presents reproductive habits that are unique among domesticated grains. Like most other grains it is capable of self-pollination or inbreeding, but individual maize plants more commonly cross-pollinate within their population. The tendency of maize to outbreed rather than self-pollinate, allows for heterosis. Often referred to as outbreeding enhancement, heterosis is a
resulting enhancement of fitness of a daughter plant relative to that of either parent due to outcrossing of the parents (Wallace et al. 2014). Factors influencing maize diversity in addition to heterosis, include the effects of pleiotropy, in which one gene is responsible for multiple phenotypes, epistasis, where two or more genes control phenotypic expression, and selection pressures by humans through the process of domestication (Wallace et al. 2014).

Generally, the maize genome is incredibly expansive and has evolved so that many small genes control a single phenotypic trait. Furthermore, different populations and varieties of maize have distinct variations in phenotypic expression of the same region of a gene. This occurs for traits such as flowering time, leaf architecture, and disease resistance (Wallace et al. 2014:32). Such plasticity in gene expression accounts for the ability of maize to adapt to regions with varying climatic and ecological factors; traits that are advantageous in one region could be deleterious in another. The wonder of maize is that it is able to select for expression of individual traits based on environmental factors; for several key traits it does not exhibit true pleiotropy (Wallace et al. 2014).

**Tehuacán Valley**

The Tehuacán Valley covers an area in highland Mexico consisting of the southern part of the state of Puebla and the northern portion of Oaxaca (Mangelsdorf et al. 1964). This area is characterized by a semiarid climate and sparse springs fed by water from the surrounding Sierra Madre Oriental Mountains as well as the Mixteca Hills (Figure 6).

Because of its location between these elevated geologic features, the Tehuacán Valley receives little annual precipitation, with 600 mm of rain fall being the average in a given year. It is important to note that all of this precipitation occurs within the short period of the spring rainy
season. During the other three seasons of the year, water is so sparse that the Valley verges on desert conditions (MacNeish 1964).

The minimal water available within the Tehuacán Valley does allow for a radiation of xerophytic plant life. Many of the plants that grow in the Valley are forced to go into a cycle of dormancy during the dry months of the year. These conditions also forced human groups to maintain very small populations, and live a nomadic lifestyle based on collection of plants and animals (MacNeish 1964; Mangelsdorf et al. 1964).

Figure 6. Environmental zones within Mesoamerica. The micro-environmental zone of the Tehuacán Valley sites, set between the Mesa Central plateau, Sierra Madre Oriental and Sierra Madre Occidental mountain ranges is denoted by the number 4. (MacNeish 1991: 84, Fig. 7).
Due to the dry climate of the Tehuacán Valley, preservation of botanical remains within archaeological contexts is rather good. Because of this, some of the oldest dated remains of maize have been identified from excavations of various cave dwellings within the Tehuacán Valley (Mangelsdorf et al. 1964). MacNeish excavated five major cave dwellings in the Tehuacán Valley (Figure 7). These dwellings span the entire Valley and encompass at least three different microenvironments (Mangelsdorf et al. 1964). The caves are Coxcatlan, Purron, San Marcos, Tecorral, and El Riego. Occupational phases from each of the caves are likewise associated with maize remains. Specifically, El Riego (200 B.C.-A.D.1500), Coxcatlan (5200-2300 B.C. and 900 B.C.-A.D. 1500), Purron (2300 B.C.-500 A.D.), San Marcos (4400 B.C.-A.D. 300), and Tecorral (only A.D. 1300) (Mangelsdorf et al. 1964).

Due to their proximity, it is likely that all of the cave dwellings were utilized by a migratory or semi-sedentary group of people, yet each of the five caves presents a unique time frame, and season of occupation. The most notable of the caves is Coxcatlan, which is distinguished by its proximity to abundant water resources, relative to the rest of the Valley. This cave is positioned near a drainage from the Sierra Madre Mountains. Access to water from this cave would have allowed for cultivation of maize during the rainy season. Mangelsdorf (1964)

Figure 7. Map of the five cave sites in the Tehuacán Valley from which remains of maize were excavated (Mangelsdorf et al. 1964: 540, Fig. 1).
suggests that cultivation would also have been possible during the dry season with the aid of irrigation.

Remains of corn were found at Coxcatlan Cave in a layer dated to 5200-3400 B.C. (Mangelsdorf et al. 1964). Botanical remains from the Coxcatlan phase are relatively uniform in size, only varying from 19-25 mm long (Mangelsdorf et al. 1964). These cobs represent an early variety of maize, as the rachises are slightly fragile. Furthermore, cobs are generally eight or four rowed with 36-72 glabrous kernels present on each cob (Mangelsdorf et al. 1964). All together, 23,607 maize specimens were collected from the cave sites in the Tehuacán Valley. Of those specimens, 12,857 were intact, or mostly intact maize cobs (Figure 8) (Mangelsdorf et al. 1964).

The Coxcatlan phase of occupation is also denoted by the presence of true manos and metates (MacNeish 1964). MacNeish marks this phase as the first at Tehuacán with “incipient
agriculture” in which microbands formed during the dry season, but macrobands were maintained in the wet season, and perhaps even annually through cultivation (MacNeish 1964).

Corn remains from the sites in the Tehuacán Valley are thought to have later given rise to two landraces of maize that are part of the “Ancient Indigenous Races of Mexico” (Mangelsdorf et al. 1964). These landraces are Nal-Tel and Chapalote. Maize excavated from the cave dwellings in the Tehuacán Valley represent the evolutionary history of the Nal-Tel-Chapalote complex of Tehuacán. This complex of extant landraces was present from around 2000-1000 B.C. in Tehuacán (Minnis 1992; Mangelsdorf et al. 1964).

American Southwest

The southwestern United States is home to a variety of cultural groups, most of which are known for their prominent use of maize agriculture. The earliest evidence of maize in the region is ca. 4000 BP, however evidence for maize cultivation increases several hundred years later (Drake et al. 2012). Pollen evidence from packrat middens on the Colorado Plateau indicate that variability in El Niño Southern Oscillation (ENSO) caused a shift from ponderosa dominated to piñon pine dominated ecosystems around 5102 cal. yr BP. This transition, prior to the introduction of maize to the American Southwest, was likely caused by a widespread aridization (Drake et al. 2012). After which, small hunter-gatherer groups cultivated the abundant piñon pines for their seeds. This practice of seed cultivation likely laid the foundation for maize agriculture to take hold once it was introduced to the region (Drake et al. 2012).

The yearly rate of rainfall in the Sonoran Desert, an area south of the Colorado Plateau, is less than 381 mm per year. The Phoenix Basin, the area of the Sonoran inhabited by the Hohokam, is on the low end of the annual precipitation spectrum, receiving about half of the average amount of rainfall per year (Fish and Fish 1992). Yet, the Hohokam were able to subsist
on the land in the Phoenix basin due to the water supply of the Salt and Gila Rivers (Figure 9). These two rivers, which are fed by mountain springs, played a central role in the ability of the Phoenix Basin to sustain life, especially the agricultural lifestyle exhibited by the Hohokam (Fish and Fish 1992) during their four main cultural phases (Figure 10).

Figure 9. Sites of importance to maize domestication in the southwestern United States and northern Sonora and Chihuahua (“Desert Borderlands”). Hohokam settlement of Snaketown, as well as the Salt and Gila Rivers are depicted. (Fish and Fish, 1994, p. 84, Fig. 1).

The Phoenix Basin is home to three distinct ecosystems, each supporting a specific set of species. These include the *Cercidium-Cereus*, a mountainous zone which consists of cacti and legume-producing small trees. Sedentary populations are not likely to be supported in this zone, as resources are available on a seasonal basis. Few maize remains have been excavated from this ecosystem, presumably because of its high elevation and the seasonal availability of its minimal
Figure 10. Chronology of Hohokam cultural phases and climate events associated with maize agriculture (Brooke 2014; Crown 1991; Pande et al. 2014)
resources (Gasser 1979). The second ecosystem is the Wash Floodplains, which provide arable land with abundant desert water sources; it is this type of environment where agriculture is most common. Over 900 kernels were collected from sites in this ecosystem through flotation. The last type of ecosystem is the Creosote Plains, an area characterized by small agricultural outcroppings. The Creosote Plains have yielded several kernel remains, but not nearly as many as the Wash Floodplains (Gasser 1979). Hohokam populations likely occupied these zones on a semi-sedentary basis, cultivating plants and making use of wild species. Cultivation of plants would give way to domestication and widespread agriculture.

Known for their agriculture, the Hohokam grew a hardy drought resistant variety of maize needing little water to reach a state of maturity. This variety is believed to be derived from the Nal-Tel-Chapalote series, a pairing of landraces developed in Mesoamerica at some point around 2,000-1,000 B.C. (Mangelsdorf et al. 1964; Minnis 1992). Shortly after their emergence in Mesoamerica, probably around 1,000-200 B.C., Nal-Tel and Chapalote migrated through the desert borderlands and into the southwestern United States. These varieties (Figure 11) were the first maize to appear in the region (Mangelsdorf et al. 1964; Fagan 2000; Minnis 1992).

Nal-Tel and Chapalote are similar to the maize remains found in Tehuacán because they are glabrous, but are characterized by their large cobs. The two races are further distinguishable by the color of their kernels. Nal-Tel kernels are orange, while Chapalote has chocolate brown kernels (Mangelsdorf et al. 1964). Furthermore, Chapalote is not a drought resistant variety of maize, but this trait is believed to have been selected for in the Chapalote genome, leading to the appearance of Maiz de Ocho, which is better suited to dry conditions (Fagan 2000).
Maiz de Ocho appeared in the southwestern United States around A.D. 700. Two complete cobs of this variety were excavated in southern New Mexico by MacNiesh (Fagan 2000). Maiz de Ocho exhibits larger kernels and has an earlier flowering cycle than Chapalote, which allows Maiz de Ocho to be more adaptable to variation in the timing of rains (Fagan 2000).

The water necessary to support agriculture in the fragile landscape of the Sonoran Desert was diverted by the Hohokam to fields through three types of irrigation technology. The first type is an extensive system of irrigation canals, which transported water from the nearby Gila and Salt rivers to fields. The second type of irrigation made use of storm runoff; it collected water from the infrequent storms in the Sonoran into shallow basins dug in the ground adjacent
to agricultural fields. The third involved capturing overland runoff and diverting it to fields using man made washes contained by large stones (Fish and Fish 2004).

A system of 500 km of canals diverted water from the Gila and Salt Rivers, transporting water upwards of 30 km from the main branch of the canal to Hohokam agricultural fields (Murphy 2009; Fish and Fish 1992). This system of irrigation implemented by the Hohokam delivered not only water to their agricultural fields, but also nutrient rich sediment suspended within that water, which helped to increase the fertility and tilth of the soil (Briggs et al. 2006; Fish 2000). Through this system of irrigation the Hohokam maintained a year-round sedentary lifestyle.

Hohokam society tended to be resilient; surpluses of food were stored and often were capable of sustaining populations for up to four years (Ravensloot et al., 2009). This planning for an uncertain future demonstrates the Hohokam knowledge of variability in Sonoran climatic conditions, or their system of scheduling. Brief fluctuations in precipitation leading to large scale but chronologically short floods and droughts were expected and the Hohokam were able to adapt to them. However, serious and prolonged periods of drought could not be accommodated through storage and planning. It is postulated that cultural shifts within Hohokam society leading to the end of the Classic period ca. A.D. 1450 were spurred by such prolonged periods of climatic variance (see Figure 10) (Ravensloot et al 2009; Clark et al. 2004; Pande et al. 2014). Periods of drought were coupled with periods of flooding of the Salt and Gila over the course of Hohokam occupation and use of the Phoenix Basin (Figure 12), thus use of irrigation and diversion of water from the Salt and Gila Rivers also varied with river discharge. The Salt and Gila rivers, which were diverted to feed the series of canals necessary to irrigate agricultural fields, are fed by runoff of precipitation in mountainous regions of the Colorado Plateau.
Thus, success of Hohokam crops was linked to precipitation in the Colorado Plateau. For example, a period of drought in the Colorado Plateau ca. A.D. 1075 (Figure 13) was felt by Hohokam peoples on the fringe of canal networks, causing Hohokam populations to consolidate toward the Salt and Gila rivers themselves, thus overloading a small area of land.

Again, around A.D. 1275 decreased moisture in the Colorado Plateau (Figure 13) caused a shift of Hohokam populations toward their population centers, abandoning peripheral settlements. However, at this time the landscape was altered severely by successive years of Hohokam agricultural practices; fields were overloaded with salts and could not produce high enough yields to sustain significant populations. This period was followed immediately by a period of high moisture ca. A.D. 1325. The sudden shift in water levels damaged canals, furthering the sequence of decline (Weaver 1972). This succession of events leading to use of all possible stores of food likely pushed Hohokam populations to depend on wild famine foods for subsistence. Ultimately, environmental variance led to the dispersal of Hohokam populations, and adoption of simpler social structure in the form of small, nucleated groups (Weaver 1972).
Maize was introduced to the Ohio Valley as early as 170 B.C. - A.D. 60 as evidenced by remains from the Holding site (Fagan 2000; Fritz 1993), but it wasn’t firmly established in the region until around A.D. 300 (Greenlee 2006). Maize from this period is generally the eight-rowed Maiz de Ocho from the southwestern United States (Fagan 2000). Furthermore, the species remained a minor crop until ca. A.D. 800-900, when it increased in frequency in the archaeological record (Fritz 1993; Greenlee 2006).

By A.D. 900-1000 the eight-rowed Northern Flint variety of maize emerged. Suited to northern climate and growing conditions, due to its adaptation for early flowering, it rapidly dominated the cultivated landscape (Smith 1989). This is coincident with the end of the Late Woodland and the onset of the Fort Ancient cultural phase, or Late Prehistoric period (ca. A.D. 1000-1450).
1000) in which wild plants and native domesticates were all but abandoned. Domesticated species exploited during this phase include the classic triad of corn, beans, and squash, as well as chenopods (Rossen 1992).

Maize faired well in the warm and wet conditions that characterized the Ohio Valley from around A.D. 350 to 1300 (Greenlee 2006). The landscape along the Ohio River is variable, including floodplains, tributary streams, and rolling hills. Regardless, the conditions of the Late Woodland period were able to support maize populations through its 140-day growing season (King 1993). Maize became the staple crop supporting life along the Ohio River by the Late Prehistoric period, around A.D. 1000, or roughly 100 years after the warm temperatures of the Medieval Climate Anomaly began to impact the world. The increased temperatures and precipitation that the Medieval Climate Anomaly offered can be seen through paleoclimatic proxy records for the Ohio Valley (Figure 14). Also, the impact of the MCA and LIA on agriculture in the Ohio Valley can be inferred (Figure 15).

Figure 14. Precipitation and temperature records for the Ohio Valley plotted against stable carbon isotope records. Climate variability is expressed in averages, with negative values indicating colder and dryer than positive values (Greenlee 2006, Fig. 16-9).
Figure 15. Chronology of Ohio Valley cultural phases and climate events associated with maize agriculture (Brooke 2014; Greenlee 2006; Smith 1989; Wymer 1993).
The divergence of maize in Mexico, and the proliferation of maize agriculture throughout the Americas were caused by innumerable factors. Mainly, these factors fit within three main categories of influence, genetics, climate, and culture. First, are the genetic elements, which include the diversity within the maize genome that allows the species to adapt to drastically different climatic zones and regions. This aspect also includes the genetic processes that led to the divergence of maize from an annual teosinte, *Zea mays* ssp. *Parviglumis*. Next, is the influence of climatic variability, which dictates the range of characteristics that may be expressed within a plant population at a given time period. Climate change events such as the Younger Dryas, the 5.1 ka aridization, the Medieval Climate Anomaly, and the Little Ice Age, all impacted expression of traits in plant populations. Last, are the cultural or human aspects, these are highly variable from region to region. However, in each of the three areas highlighted in this study, the pressures of human selection and patterns of scheduling caused an adoption of maize agriculture. Each of the three regions examined represents a different response to the same basic factors influencing maize agriculture.
Chapter V
Analysis

When examining the transition of a culture from hunting and gathering, to cultivating, and finally an agricultural system, it is absolutely necessary to take into account local environmental and global climatic conditions. The ability of individuals to act as decision-makers in their interactions with plants should always be examined in conjunction with the concept of environment dictating the range of expressed traits within a population of plants.

Together, these elements reveal a system by which cultures alter, adapt to, and interact with their environment. Systems such as this can be explored through application of a theoretical model (Figure 4) to cultures known for adopting intensive agriculture. Specifically, this study examines groups in the Tehuacán and Balsas River Valleys, the American Southwest, and the Ohio Valley are examined. This is done in an attempt to understand four main queries: (1) How did maize diverge from teosinte in Mesoamerica and what impact did changing climate have in this transition? (2) What roles did humans and climate play in the northward diffusion of maize? (3) To what extent has maize morphology changed over the course of its history and geographic range as a species, and what pressures contributed to these morphologic changes? (4) How did social structure within human populations change as maize was introduced and eventually became a staple crop?

The model outlined in Chapter Two explains these interactions by means of seasonality, scheduling, and feedback within an interactive system of plants, people, and environment. Thus, in its explanation of biological changes resulting in the speciation and adaptation of maize, it incorporates global climate forcings, regional ecosystem variation, and cultural adaptations. These events are examined in conjunction with detrimental societal changes, like the decline in
population and prominence of a cultural group, which is representative of positive feedback or a transition to a new adaptive strategy. This is not done as a basis for the perpetuation of collapse narratives, but as a way of understanding the magnitude of the environment’s influence on human groups.

Maize agriculture moved throughout the Americas by way of interactions between or migrations of cultural groups. Changing climate heavily influenced the domestication of maize and its emergence as a genetically and morphologically distinct species. However, changing climate did not necessarily drive the introduction of the species to new areas. There is no evidence of dramatic variation in climate prior to, or contemporaneous with the introduction of maize to either the American Southwest or the Ohio Valley. Rather, I hypothesize simply that seasonal migrations or trade between cultural groups, motivated by the needs and scheduling of each culture, were the forces behind the introduction of maize agriculture to different regions.

In this scenario, as maize moved from one region to another, the species often experienced climatic conditions outside the parameters of its previous range of habitation. Fluidity in the genetic structure of the species allowed it to develop adaptations relatively rapidly that were specific to the demands of the ecosystem and climate of a new region. Thus, as the model dictates, the climate of a new region impacted the seasonality of the plant. Furthermore, after maize fully adapted to its new environment, human groups formed patterns of scheduling based on the availability of the species. Once maize agriculture took hold in a region, the species was susceptible to any deviations from the “normal” climate of that area, or deviations from equilibrium.

The influence of climate changes following intensified dependency on maize as a staple crop are more evident than the influence of climate changes being a factor leading to the
introduction of maize to a region. These changes can be viewed as a perturbation to the system. If the system in question displays resiliency, then negative feedback occurs and the present equilibrium will be maintained. However, if the system is not resilient, then positive feedback occurs and results in the development of a new equilibrium.

**Genetic and Climate Factors in the Emergence of Maize**

Maize emerged in the Central Balsas region of Mexico under climatic conditions of the early Holocene around the time of the glacial termination event, the Younger Dryas (ca. 11,500 BP) (Piperno 2014). The development of maize from a variety of annual teosinte, *Zea mays* ssp. *parviglumis*, is understood to be greatly influenced by the specific changes in climate presented by the termination of the Pleistocene and onset of the Holocene. Specifically, levels of atmospheric carbon dioxide (near one third higher), along with increased average temperatures, and an overall rise in precipitation (by a factor of 20-40%), allowed for variation in the traits expressed by maize precursor *Zea mays* ssp. *parviglumis* (Piperno 2014). This new range of gene expression enabled novel interactions between the species and human populations, which likely led to practices of cultivation and the eventual domestication of maize. Thus, as the model indicates, environmental and climatic conditions dictate the availability of resources, but more importantly they allow for expression of a specific range of traits that are best suited to the conditions.

However, these changes in gene expression by teosinte alone do not explain the emergence of maize. These environment-influenced modifications must be examined in conjunction with an understanding of the selection pressures caused by human utilization of natural resources. It is these pressures that cause specific traits expressed by maize to be selected for and grow to dominate a population. The clearest example of this is the evolution of kernel
size over time. Larger kernels are advantageous to human populations because they provide an increased volume of nutrition as compared to small kernels. The transition from the original, small kernelled maize to massively kernelled maize varieties such as Nal-tel-Chapalote, can be observed in botanical assemblages in Mexico (Fagan 2000).

Over time, these processes deviate from the original system so that balance may be achieved again in an altered system. The model explains this as positive feedback, or deviation from equilibrium in the form of amplification. In this instance, the positive feedback caused by human interactions with plants resulted in the emergence of *Zea mays* L. This system intensified, eventually causing subsistence systems to change within a culture, and the adoption of widespread agriculture.

**Tehuacán Valley**

The Tehuacán Valley does not seem to be the most hospitable of environments, but it is surprisingly adept in its ability to support life for sustained periods of time. The first evidence for occupation of the Valley comes from the end of the Pleistocene. It is undoubted that the first occupants of the Valley consisted of small migratory microbands living quite possibly in near starvation conditions during the dry parts of the year (MacNeish 1964).

However, as deposits from later periods are examined it is clear that the groups residing in the Tehuacán Valley, through altering their patterns of scheduling, began to experiment with plant cultivation. The presence of early varieties of four rowed maize on cave floors from the Coxcatlan occupation (5200-2300 B.C.) indicate occupations of larger numbers of people during the wet season, and some annual camps of macrobands (MacNeish 1964; Mangelsdorf et al. 1964). The manipulation of plants, namely teosinte, caused adaptations beneficial to humans but deleterious in the wild (like the removal of hard glumes around kernels) to be selected for (Tian
et al. 2009). This process of cultivation led to the emergence of domesticated species like maize, and eventually full-scale agriculture. These changes indicate both a need for increasingly reliable food sources to mitigate the risk of variability in seasonal availability of wild plants, and an awareness of basic processes of germination.

Human selection of specific plants within an environment is directly related to changes in patterns of scheduling as well as patterns of social structure within cultural groups occupying the Tehuácan Valley. This cycle of human selection leading to changes in patterns of scheduling and social structure continues in a positive feedback loop, which functions to accelerate changes in both social structure and cultivation practices. This pattern, after thousands of years, gives way to the classic highland Mexico agricultural and social structure in which “secular cities” develop with widespread systems of irrigation and complex ceremonial and social structures (MacNeish 1964).

**American Southwest**

The Phoenix basin is an arid environment containing pockets of precipitation during select months, and providing otherwise harsh living conditions. The local flora provide few plants with the prospects of being cultivated to the point of domestication. The devil’s claw is suggested to be the only locally domesticated plant within the southwestern United States (Ford 1981). Because of the harsh environment and minimal resources, it is not difficult to assume that maize, and other domesticates such as squash and gourd (whose introduction to the Southwest are dated to around the same time period as that of maize), would have proved appealing to cultural groups living within this landscape.

An aridization event triggered by altered patterns in ENSO occurred across the American Southwest around 5102 cal. yr BP. The dry conditions of this event altered the ecological balance
within the region by causing a shift from ponderosa pine dominated ecosystems to piñon pine
dominated ecosystems (Drake et al. 2012). The increased prevalence of piñon pines constituted a
shift in seasonally available resources within the region. Thus, human groups altered their
patterns of scheduling to include cultivation of piñon nuts. Cultivation of plants allows for
groups to increase their ability to control scheduling, and increases predictability of harvest from
season to season. This change in behavior allowed for maize cultivation, and later agriculture to
take hold in the region once the species was introduced (Drake et al. 2012). Furthermore, the
domestication of plants increases the degree of human selection pressures. For example, the
Hohokam were able to cause traits such as drought resistance and larger kernels size to be
selected for in Maiz de Ocho (Fagan 2000).

Once Hohokam populations transitioned from migratory or semi-sedentary bands to a
sedentary population, they were characterized by a complete dependence upon maize to support
their population. Maize was of such necessity to sustaining population size and elements of
Hohokam social structure that they were known to store up to a four year supply of maize at a
time. It is believed that this scheduling practice was done out of Hohokam understanding of the
likelihood of extreme variation in environmental conditions (especially precipitation, and river
discharge) and the influence they have on maize agriculture (Ravensloot et al. 2009). In the end,
it was the unpredictability of river discharge, spurred by climatic variation over the course of the
Medieval Climate Anomaly and the Little Ice Age, that caused a series of long droughts coupled
with a large-scale flooding event (Figure 12) (Clark et al. 2004; Pande et al. 2014; Ravensloot et
al 2009).

It has been noted that the efficiency of Hohokam irrigation and agricultural practices led
to an increase in Hohokam population during the period A.D. 600-1050 (Johnson 1997).
However, the landscape the Hohokam inhabited was not able to support such a large population (Fish 2000). The dramatic increase in population gave way to negative feedback. In this scenario, the stimulus of population increase created a greater need for food resources and thus an increased intensity of agriculture. However, as the intensity of agriculture increased, the yield actually reduced due to a depletion of soil nutrients.

Ultimately, feedback in the system led to an alteration in the balance of the local ecosystem, preventing it from sustaining considerable human populations through agriculture. This rendered the Hohokam unable to recover their previous system and positive feedback allowed adoption of a new system with fewer connections. This processes is seen in the abandonment phase of Hohokam cultural chronology (Figure 10). There is no evidence of Hohokam habitation of southern Arizona after A.D. 1450 (Fish and Fish 1992). Modern research suggests that the Hohokam fractioned into small successor groups. However, none of these groups were able to replicate the complexity of Hohokam settlement patterns, agriculture, political and community structure, or population size (Fish and Fish 1992). Nor were they able to successfully return to a pre-agricultural nomadic lifestyle.

**Ohio Valley**

The Ohio Valley presents the most intriguing case of the three regions examined in this study. This region is the only one of the three that had a well-established agricultural complex prior to the introduction of maize to the area. Thus, the behaviors of cultivation and more importantly, agriculture were already known and practiced by the cultural groups residing in the Ohio Valley. This makes for an interesting comparison, and offers an example of the breadth of scenarios the theoretical model is able to assess.
The oldest evidence of maize in the region is eight-rowed Maiz de Ocho dated to 170 B.C. – A.D. 60 (Fagan 2000; Fritz 1993). This variety is the same as that which flourished in the American Southwest. However, it was not entirely suited to the humid conditions of the Northeast. Thus, maize did not become widespread until around A.D. 300 (Greenlee 2006) and maize agriculture did not supplant the traditional crops of the Eastern Agricultural Complex until hundreds of years later, ca. A.D. 800-900 (Fritz 1993; Greenlee 2006). This period of relative dormancy of maize in the region is representative of the time necessary for pressures of natural and human selection to act on the species in the process of selecting for traits best suited to the environment. Thus, once enough advantageous traits accumulated by means of human and environmental selection pressures, a variety of maize able to thrive in the humid, wet conditions of the Ohio Valley developed. This landrace grew to rapidly dominate the landscape once human populations sufficiently altered their patterns of scheduling to accommodate for maize. This is seen with the influx of eight-rowed Northern Flint corn in the botanical assemblage by A.D. 900-1000 (Greenlee 2006).

Precipitation, the seasonal cycle of rainfall, and the 140-day growing season characteristic in the North are the main factors influencing the ability of maize to reach maturity in this climate. Once maize adapted to the warm and wet conditions of the Ohio Valley it was used to support large populations. Botanical assemblages in the Ohio Valley suggest that by A.D. 1000 maize dominated the diet of those who resided in the Valley. This time is contemporaneous with the onset of the Fort Ancient cultural phase (Smith 1989).

The intensification of maize agriculture in the Ohio Valley is also closely linked to the timing of the Medieval Climate Anomaly, and the increase in precipitation it offered (Figure 14). Increases in the consumption of maize, as evidenced by levels of collagen $^{13}$C (Greenlee 2006)
occur ca. A.D. 900, corresponding with the onset of the Medieval Climate Anomaly (Figure 15). The conditions of this period of rapid climate change allowed for changes in seasonal abundance of maize, which were likely followed by the adaptation of scheduling patterns by humans.
The research within this study was driven by several overarching questions. These include (1) How did maize diverge from teosinte in Mesoamerica and what impact did changing climate have in this transition? (2) What roles did humans play in the emergence and diffusion of maize, specifically diffusion to the American Southwest and the Ohio Valley? (3) To what extent has maize morphology changed as the species navigates time and space and what pressures contributed to these morphologic changes? (4) How did social structure and behavior patterns within human populations change as maize was introduced and eventually became a staple crop in an area? In essence this study seeks to identify the qualities that make maize so adaptable to various regions and climatic conditions throughout the Americas, and how qualities impact and are impacted by human populations, as well as variation in climatic conditions.

A model for an interactive system of plants, people, and environment, wherein interactions are explained in terms of seasonality, scheduling, and feedback within the system was employed in this study. Together, these elements reveal a system by which cultures alter, adapt to, and interact with their environment. This encompasses transitions such as those between hunter-gatherer and intensive agricultural subsistence strategies. This model emphasizes the importance of acknowledging the ability of individuals to act as decision-makers in their interactions with plants, which is examined in conjunction with the concept of environment dictating the range of traits expressed within a population of plants. Thus, the model incorporates global climate forcings, regional ecosystem variation, and cultural adaptations in its explanation of the speciation and adaptation of maize to different regions throughout time.
Data for this study was acquired through a process of literature review. The data revealed several trends in the adoption of maize agriculture between the three regions. These include, (1) the existence of a lag period between the initial introduction of maize to an area and the adoption of maize agriculture on a large scale by a cultural group, (2) a flexibility in the genetic structure of maize allowing for adaptation to the specific environmental conditions of each region, (3) a transition to widespread dependence on maize as the staple food source for cultures after they adopt maize agriculture on a large scale; this change leaves cultural groups vulnerable to long term or severe changes in climatic patterns.

Maize was first cultivated in Mesomarica. The domestication of maize from a wild species of teosinte, generally accepted to be *Z. mays* *ssp. parviglumis*, most likely occurred in the Mesoamerican lowland region of the Balsas River Valley. Yet, the highlands of Mesoamerica specifically, the Tehuacán Valley, yield some of the oldest archaeological remains of maize and evidence of maize cultivators. Maize was domesticated in the context of early Holocene climate variability. Expression of novel traits by plant populations influenced by these climatic shifts encouraged human selection toward the evolution of maize. The Younger Dryas (YD) is an early Holocene (11,500 BP) period characterized by low temperatures and low precipitation (Hetherington and Reid 2010; Brooke 2014). The cool and dry conditions of the YD provided an environment uniquely suited to early domestication of plants like maize (Hetherington and Reid 2010; Brooke 2014; Piperno 2014).

After its initial domestication, maize agriculture took hold throughout Mesoamerica, and was then transmitted north and south via human migrations and interactions. The northward progression, which is examined in this paper, exposed maize to novel environmental zones. Case studies of maize agriculture in the American Southwest, and the Ohio Valley underscore the
fluidity of maize as a species through its ability to adapt to these new regions. In each of these new regions local human populations adopted maize agriculture after a period of time. Furthermore, the success of the crop was dictated by both human action, and environmental controls. Particularly, the Medieval Climate Anomaly, and the Little Ice Age played a part in the longevity of large-scale maize agriculture in these regions. Furthermore, the 5.1 ka aridization event led to the adoption of piñon cultivation practices in the American Southwest, which allowed for ease in the adoption of maize cultivation when the plant was introduced.

All of the locations studied display a lag time in which genetic changes built up within the species until it was well adapted to its new environment. Overall, maize displays an incredible diversity of expressible traits within its genome, allowing it to respond to environmental and climatic shifts in seasonality. This process is accelerated by means of human selection for traits that are beneficial to supporting large populations.

The diversity of traits exhibited by landraces within the *Zea mays* species reflects the genetic flexibility of the plant. These genetic characteristics allow maize to be flexible in gene expression. Genetic studies allow us to see the degree of flexibility maize possesses as a species. It is this genetic flexibility that causes maize to be highly adaptable, and thus of the utmost importance to human populations. Maize continues to sustain human groups, now more than it ever did in antiquity. Understanding of the divergence of maize, and its adaptability are key to perpetuating its modern use. However, most important is maize’s relationship with the environment in the past. It must be remembered that societies have been built on the shoulders of maize agriculture many times over, and they continually fall victim to unexpected climatic changes. This study shows that the genetic structure and flexibility of maize allow humans to manipulate and benefit from it. Yet, regardless of genetic flexibility, both plant and human
populations are subject to the impacts of dramatic, or even slight variations in the overarching climatic system of the Earth.
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Suggestions for Future Research

To future maize enthusiasts, I would suggest that you gain as thorough a background as possible in plant systematics, specifically theories of genetic inheritance. This study was limited by my minimal knowledge of modern concepts of genetics, specifically those of evolutionary developmental biology (EvoDevo). This field constitutes the newest, most groundbreaking studies in plant genetics (see Piperno 2014). Yet, understanding the foundations of both the teosinte hypothesis vs. hybrid hypothesis and the lowland origin vs. highland origin hypothesis debates is necessary to comprehend modern research on maize domestication.

Additionally, I suggest that you delve deeper into domestication and all of the components of culture it influences in a single region, rather than multiple. Doing so will allow you to understand the region and culture, as well as how they change, holistically.

Last, I highly recommend that you try to gain some experience with actual botanical remains. This is probably the most difficult of all three suggestions, yet it can be done. Understanding the processes used in paleoethnobotanical studies first-hand will overwhelmingly aid in your understanding of the literature.