Population trends and the transition to agriculture: Global processes as seen from North America

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Agriculture—specifically an intensification of the production of readily stored food and its distribution—has supported an increase in the global human population throughout the Holocene. Today, with greatly accelerated of growth during recent centuries, we have reached about 8 billion people. Human skeletal and archaeobotanical remains clarify what occurred over several millennia of profound societal and population change in small-scale societies once distributed across the North American midcontinent. Stepwise, not gradual, changes in the move toward an agriculturally based life, as indicated by plant remains, left a demographic signal reflecting age-independent (α_2) mortality as estimated from skeletons. Designated the age-independent component of the Siler model, it is tracked through the juvenility index (JI), which is increasingly being used in studies of archaeological skeletons. Usually interpreted as a fertility indicator, the JI is more responsive to age-independent mortality in societies that dominated most of human existence. In the midcontinent, the JI increased as people transitioned to a more intensive form of food production that prominently featured maize. Several centuries later, the JI declined, along with a reversion to a somewhat more diverse diet and a reduction in overall population size. Changes in age-independent mortality coincided with previously recognized increases in intergroup conflict, group movement, and pathogen exposure. Similar rises and falls in JI values have been reported for other parts of the world during the emergence of agricultural systems.

age-independent mortality | paleodemography | agricultural transition | eastern North America

Fueled by a capacity to intensify food production through agriculture, which only occurred during the Holocene, human populations today far surpass what our foraging predecessors could attain even under the most favorable circumstances. Much of this increase—there are now about 8 billion of us, a few thousand times the population at the start of the Holocene—took place from the industrial revolution onward. Yet millennia earlier, there was also an uptick in numbers that accompanied the emergence of agricultural economies and, later, sociopolitical systems referred to as states or civilizations (1–5).

Two centuries ago, Malthus (6) influentially, if controversially, noted the far-reaching consequences of the relationship between the number of mouths to feed and the food available to do it. Surely the preindustrial intensification of food production and a capacity to store surpluses influenced population growth. There remains, however, great uncertainty about precisely how it happened, when it did so, and causal relationships among technological innovations, societal organization, and demographic regimes (7, 8). Understanding what occurred can only be based on compiling data from numerous sites in archaeologically well-documented regions.

The relationship between the intensification of food production in preindustrial societies and one aspect of mortality, the age-independent risk of dying, is clarified by examining archaeobotanical and skeletal remains from sites in the archaeologically well-characterized North American midcontinent. This region is one of the independent centers of plant domestication (9–12). Centuries after native cultigens, collectively the Eastern Agricultural Complex (EAC), became widely used, people began to rely heavily on maize and beans, introduced plants (IPs) that by the historic period had become dietary mainstays. This transition to agricultural economies—first to native plants and then to IPs (9–12)—is accompanied by a distinguishable demographic signal in skeletal samples.

A change in age-at-death distributions is captured by a skeletal indicator that is seeing increased archaeological use: Bocquet-Appel's (13) juvenility index (JI). Previously interpreted as a measure of fertility (13), and hence population growth, its interpretation is shown to be more complicated. The JI is, in fact, a better proxy of age-independent mortality in demographic regimes that characterized much of human existence. In the midcontinent, the move to agriculture was accompanied by changes in age-independent mortality as quasi-sedentary hunter-and-gathering ways of life were replaced by those featuring a heavy reliance on the EAC and, later, IPs.

Significance

One of the most profound transitions in human existence was the development of agriculture. It fueled an increase in the global population that culminated in the unprecedented growth of recent centuries. Growth at the outset, however, was quite slow. In the North American midcontinent, the early move toward agriculture was associated with changes in age-independent mortality. It dampened the potential for unrestrained population growth following the development of new systems of food production. The overall pattern of change in age-independent mortality is for the first time tied to an archaeological measure of food production.

Population and Agriculture

It is generally understood that population growth was associated with the emergence of socioeconomic systems that facilitated a higher caloric return per unit of land and the capacity to distribute large quantities of food. These developments accompanied greater inequality within ancient states that internally were politically, socially, and economically differentiated. Regardless of whether socioeconomic changes were a cause or consequence of population growth, and it is unlikely directions of causation can be so neatly separated, demographic estimates are critical to furthering our understanding of cultural trajectories, host-pathogen coevolution, human genetic diversity, and our species' environmental impact on local to global scales. Unfortunately, much less solid information is available on preindustrial population histories, including what took place and why it happened, than one might imagine.

Where agriculture developed independently, beginning as much as 10 millennia ago, the intensification of food production spanned long periods of time, with worldwide innovations continuing up to today (11, 14, 15). The early development of agricultural economies was variable within and between regions, and it did not follow an unwavering unilinear path toward ever-greater reliance on domesticated plants and animals. For much of this time, people cannot be neatly separated into those who relied on foraging or farming, because food-acquisition strategies featured elements of both (15).

The agricultural transition had far-reaching effects beyond dietary composition. A capacity to greatly modify a community's immediate surroundings, notably through land-use practices leading to ecosystem changes, has been proposed as marking the boundary between the Holocene and the Anthropocene (16). Although there is no agreement about precisely when the Anthropocene might be said to have begun, long-lasting alterations of local environments, including deforestation and soil erosion, negatively affected small-scale societies in the distant past (17). Here population histories are important, if for no other reason than large numbers of people have a greater impact on their surroundings than fewer people who live in much the same way.

With the emergence of organizationally complex societies referred to as states, populations continued to increase long after agricultural systems were firmly established (2). Societies became larger, and urban centers appeared that eventually increased in number and size. These societies had a potential to intensify food production and, critically, to distribute the results of those efforts to the people that needed them, despite inequities that were as great as, if not exceeding, those of today.

The presence of ever-increasing numbers of people globally is commonly said to have been accompanied by greater sickness and earlier death (18, 19). These Malthusian (6) "positive checks," or "misery," failed to halt population growth, although they must have dampened it. Such miseries surely capture a sense of what innumerable people experienced. Malnutrition, infectious diseases, and premature death are said to have contributed to a progressive decline in the human condition, beginning with agricultural economies and continuing with the emergence of complex sociopolitical systems. Such a simple and universal monotonic decline in the human condition, however, suffers from theoretical, methodological, and empirical (including sampling) problems (20–22). The evolutionary processes were likely more complex and featured greater geographical, temporal, and cultural variability in health, however measured, than is popularly thought.

Pace of Change. For humans, natural increases resulting in logistic growth where population expansions are dampened through density-dependent controls, such as food shortages, can resume again once limitations on further growth are circumvented through cultural innovations. Resource caps on population growth and technological developments spurred by that very same growth are positions famously attributed to Malthus (6) and Boserup (23). Often contrasted with one another, their positions are arguably complementary, with alternating periods of demographic and economic stasis and expansion (8, 24). There is, in fact, some empirical support for such growth among hunter-gatherers (25).

From an archaeological perspective, stepwise changes should be expected over the long course of human existence, not readily dismissed as a lack of intermediate stages in what otherwise would be gradual transformations. Technological innovations, seasonal allocations of labor, group mobility, and the like are integrally linked to one another. There comes a time when incremental changes are no longer sufficient to accommodate the pressure to produce, necessitating major societal transformations. But the numbers of people, to which can be added sociopolitical complexity, did not simply increase monotonically over time. Archaeological evidence indicates there were major downturns in population size across broadly defined regions involving early farming societies to those of classical antiquity (26–28).

Regardless of how it took place, preindustrial population growth in subcontinental or larger regions was incredibly slow for virtually all of our species' existence (2, 4, 29). Yet current evidence points to varied histories of expansion and contraction. The direction and magnitude of change in population size have been monitored in recent years through compilations of radiocarbon dates serving as population proxies (27, 30, 31). However, tabulations of radiocarbon dates, sites, or any other such archaeological material are not informative about the specific shifts in demographic regimes that led to change over time in population histories. Tackling that particular problem is somewhat simplified by reducing it to fertility and mortality, not migration, as long as sufficiently large geographical areas are examined.

Age-Independent Mortality. Given the remarkable human capacity to adapt to local settings, it is unclear what regulated overall growth to approximate zero. It has yet to be explained how birth and death rates could have been precisely balanced throughout the world for generations on end, and modeling shows it was unlikely (32). Perhaps periodic population-wide crashes, which undoubtedly varied in magnitude and frequency, contributed greatly to reducing the overall number of people, depressing otherwise positive growth rates and threatening the very existence of negatively trending groups (32). In self-supporting communities, excess adult deaths would affect the capacity to recover quickly and contribute to downstream mortality among dependents, most importantly children, who could no longer be adequately supported.

To identify if catastrophic mortality—an approximation of age-independent mortality where everyone experienced an elevated risk of dying—left a distinguishable signature in skeletal samples, researchers have focused on mortality profiles (33, 34). The goal is to find a distribution of skeletons that departs from what might be produced through the normal attrition of a cohort as it ages. There is merit in that approach when all burials took place over a short period of time, as might happen after a village massacre or a particularly lethal epidemic. But distinctions between attritional and catastrophic mortality profiles are

not always clear cut. Within a single cemetery, the graves for disaster victims can be mixed among others holding the remains of people who, in aggregate, represented the deaths that normally accumulate over time (35). In short, we known next to nothing about whether events that caused excess mortality were common or infrequent during the great majority of human existence.

One way to address this limitation is to examine the age-independent (α_2) component of the Siler model. The model also features exponentially declining juvenile and exponentially increasing adult components (i.e., negative and positive Gompertz distributions) (36, 37). Decomposing mortality into its constituent parts within the Siler model only tells part of the demographic story. There were times, for example, when fertility was likely an important driver of population growth. Nevertheless, age-independent mortality provides important perspectives on the human experience, including how it changed over time and the risks people faced.

In archaeological contexts, an increase in age-independent mortality might be attributable to recurrent, highly transmittable, and severe infectious diseases where their spread was facilitated by regional trade networks or tightly integrated political systems (38, 39). Cultural behavior can also play a part in it through excess mortality in age groups where deaths are typically infrequent, notably among adolescents and young adults. In early agricultural societies, for example, it might have been an outcome of warfare or heavy labor demands that fell disproportionately on those who were physically the most capable. An indicator of age-independent mortality does not tell us what caused the deaths. But it does provide a means of assessing the degree to which various human groups were prone to such mortality.

Archaeological Indicators

Skeletal Remains. Measuring change over time in age-independent mortality requires many culturally well-characterized skeletal samples. Unfortunately, such samples are unevenly distributed over time and space, they tend to be small, and age estimates are often inaccurate and biased, especially for adults aged through senescent changes (40). A systematic underestimation of older adult ages is a major reason various single-figure proxies of demographic processes have been proposed (13, 39, 41). Omitting the youngest children, particularly infants, accommodates their underrepresentation from culture-specific burial practices, poor bone preservation, and inadequate excavation procedures.

Here we use Bocquet-Appel's (13) JI that excludes deaths during the first 5 y of life (13). It is associated with crude birth and population growth rates in simulations based on stable populations (13). The JI has consequently been interpreted as an indicator of fertility; hence, population growth since the proportion of juveniles relative to adults in death assemblages is indicative of such growth. But here it is shown that the JI is more responsive to variation in age-independent mortality (*SI Appendix,* section 1).

The JI can be understood as follows, starting with the hazard of dying at age x ($h(x)$), the number of people in a stationary population at risk for dying at age x (l_x), and time treated as a continuous variable. In this instance, the hazard ($h(x)$) comes from the Siler model, where age-independent (α_2) mortality is of special interest. In a stationary population, the frequency of people of age x who are at risk for dying is $l_x = e^{\int_0^x h(y)\,dy}$. The formula can be modified to accommodate a stable population's nonzero constant growth rate (r), $l_x^r = (1-r)^x \cdot e^{\int_0^x h(y)\,dy}$. The JI, taking into account population growth, the hazard, and

the people at risk for dying, is $D_{5-20} = \int_5^{20} l_x^r \cdot h(x)\,dx$ divided by $D_{5+} = \int_5^\infty l_x^r \cdot h(x)\,dx$. Here r indicates change in the size of consecutive birth cohorts. It follows that when r exceeds zero, the population grows. When substantial population growth does not occur during a period of increased fertility, the pattern of mortality cannot remain constant. Age-specific mortality rates change, a deviation from the stable population model when applied to a group of skeletons that accumulated over time.

Of particular importance are situations where the intrinsic growth rate is close to zero. They would include many archaeological samples that consist of deaths that took place over numerous generations, up to several centuries or more. Given the problematic nature of archaeological data, it is important to note that the JI permits the collection of information from many samples distributed across large geographical areas and long time periods. Numerous cemeteries are needed to track central tendencies in population characteristics.

Archaeobotanical Remains. For much the same reason, measures of socioeconomic change are needed to take advantage of meticulously detailed, but variably reported, site-specific information from decades of archaeological investigations. Here plant remains serve as a proxy for overall subsistence systems. In eastern North America, the agricultural transition involved the cultivation of plants uncomplicated by animal husbandry, simplifying the monitoring of changes in subsistence practices.

We focus on the proportions of archaeobotanical remains for three reasons. Our concern is with the agricultural transition that, in eastern North America, involved native and introduced cultigens. Charred plant remains are generally abundant at archaeological sites, especially those dating to the last several thousand years. Archaeobotanical material has been a major focus of research in the midcontinent for the past half-century. These remains, therefore, are ideal for tracking changes in food-acquisition systems from hunting-and-gathering societies to those based on subsistence agriculture.

The first proportion is all cultigens (EAC and IPs) relative to cultigens plus wild plants, with nuts serving as a measure of the latter. It captures the initial transition to the intensive use of native species, as well as what took place afterward. The second is maize plus beans, the two IPs, relative to all cultigens (EAC and IPs). It measures the move to plants that figured prominently in historic period subsistence strategies, a shift that took advantage of an already well-established cultivation system. These data do not represent the proportions of plants actually eaten. Charred plant remains cannot be translated directly into dietary composition. Nevertheless, marked changes in the species composition of samples from diverse environmental and cultural settings signal widespread changes in subsistence practices.

When archaeobotanical data are distributed in a temporal sequence, a continuous process of incremental adjustments can be contrasted with one that took place in fits and starts. The latter would be visible as a series of relatively rapid episodes of change punctuated by periods of near stasis.

North American Midcontinent

Despite variation in the size and sociopolitical complexity of contemporaneous midcontinental societies, they shared many cultural traditions and followed similar evolutionary trajectories (42). Conventionally classified as tribes and chiefdoms, there was considerable overlap among them, regardless of how they might be categorized. They included some of the largest and
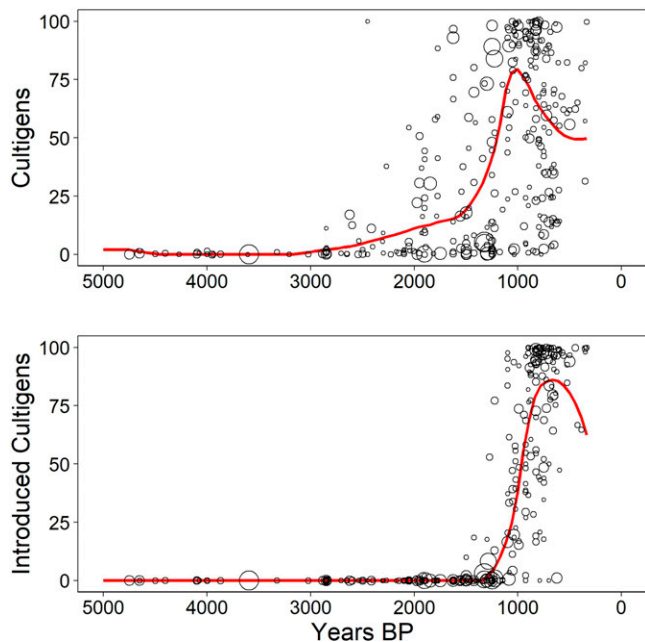
Fig. 1. Change over time in all cultigens relative to cultigens plus wild plants, represented by nuts (*Top*), and the introduced crops maize and beans relative to all cultigens (*Bottom*). Variation in sample sizes is indicated by different-sized points, and loess smoothed curves are weighted by sample size. The transition to more intensive food-production systems was not gradual but instead took place in a stepwise fashion.

most powerful societies in precontact eastern North America, referred to archaeologically as Mississippian.

In the midcontinent, native and introduced cultigens were incorporated into diets at different times. Initially, several native plants that are prolific producers of starchy and oily seeds, with some regarded as domesticates, were cultivated (9–12, 43). Maize and beans, introduced later, were grafted onto existing cultivation practices. Yet however much people relied on cultigens, wild plants and animals continued to be a major part of diets into the historic period (44, 45).

About 2 millennia ago, there was an uptick in the representation of native cultigens at many sites (Fig. 1). It postdated by 2,000 y or more the earliest domesticated native plants, as indicated by morphological changes in several species (9, 10, 43). The samples in Fig. 1 conform to a previously noted abundance of starchy and oily seeds from sites that are as much as 2 millennia old, although the dominant EAC species varied from one place to another (9–11).

The widespread establishment of native plant cultivation was followed less than a millennium later by a heavy reliance on introduced crops. Although data in Fig. 1 include beans, the IP figures are essentially a maize signal, because beans, introduced several centuries after maize, are poorly preserved in archaeobotanical assemblages. This second change in archaeobotanical sample composition is consistent with a previously recognized lag between the establishment of cultivation systems based on the EAC and the adoption of maize (9–11). The move toward greater reliance on maize is also indicated by stable carbon isotope data from human skeletons (46–48).

Although widespread shifts in plant use are apparent when archaeobotanical samples are viewed collectively, throughout the process of cultigen adoption there was considerable variation among sites. It reflects, however imprecisely, dietary preferences, local environmental settings, and long- and short-term variability in ever-fluctuating resource availability. Such differences are

expected of communities that relied on what was available nearby, hence a need for large numbers of sites to detect general tendencies on the long stepwise road to agricultural economies. The plant remains are consistent with stable carbon isotope results that indicate variation in maize consumption among late precontact groups, including people who occupied geographically and temporally proximate sites (47, 49–52). Such differences are at least partly reducible to locally distinctive ways of life and settlement size, both affecting the immediate environs of sites.

Despite a rapid increase late in the first millennium CE in the representation of cultigens in diets, including maize, only a few centuries later they had declined in importance (Fig. 1). The results support an earlier stable carbon isotope analysis of teeth, where maize consumption, after reaching its peak, dropped during the period when the cultigen fraction of archaeobotanical samples also declined (53). This shift in dietary patterns is likely attributable to both demographic and cultural developments that were well under way by that time. The final centuries of the precontact period saw a marked decline in population, including wider spacing of occupied places, the dissolution of formerly strong Mississippian chiefdoms, greater group movement, and intense warfare (26, 42, 54–57). There were also prolonged droughts accompanying the transition to the Little Ice Age, although there was subregional variation in their timing and severity (55, 58–60). Societal instability was attributable to a concatenation of environmental and social pressures, including climatic downturns, notably the risk of back-to-back crop failures, factional competition within societies, and conflict among spatially discrete groups of people. A marked thinning of the population, which had begun by the 13th century CE, was associated with a partial return to a life based on wild resources, as indicated by the archaeobotanical data.

For the skeletons, the central tendency in JI figures indicates that age-independent mortality did not remain fixed over time (Fig. 2). Little can be said about the first several millennia, a period dominated by quasi-sedentary hunter-gatherer societies, other than the JI figures exhibit considerable variation. There are not enough samples to detect temporal patterns. Differences

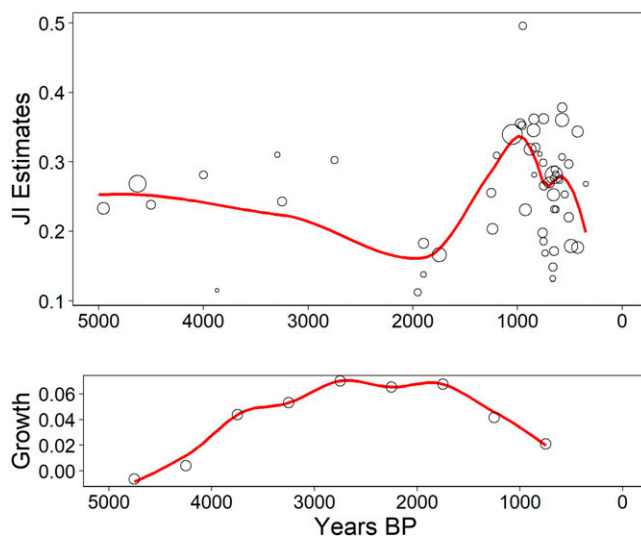**Fig. 2.** Change over time in the JI, an estimate of age-independent mortality (*Top*), is shown by a loess smoothed curve weighted by sample size. Skeletal sample sizes are indicated by different-sized points. Intrinsic population growth (as a percentage) at 500-y intervals (*Bottom*) is estimated from archaeological sites in eight states in eastern North America (42). Three states are entirely encompassed by the study area.

among the samples presumably result from some combination of archaeological sampling, bone preservation, and life experiences.

A decline in the JI, which reached a low point approximately 2 millennia ago during the Middle Woodland period, coincides with an increase in native cultigen consumption by many societies (Figs. 1 and 2). The shift in subsistence practices, even if the plants were mainly a means of blunting the worst effects of seasonal shortages (9), was sufficient to reduce age-independent mortality. Deaths directly or indirectly attributable to food shortages would have been a likely cause of such mortality, so resource-related hardships were seemingly not as severe or frequent as those experienced by earlier hunting-and-gathering populations. For about a half-millennium, there were impressive increases in mound and earthwork construction, a greater intergroup exchange of raw materials and symbolically charged artifacts, more permeable boundaries between spatially discrete groups, and a decline in warfare (42, 61, 62). Subsistence changes would have resulted in less pressure on local resources through the productive and storage potential of native cultigens. A more stable and sure food supply provided opportunities for leaders to orchestrate large ceremonies, which sometimes involved building massive earthen monuments, while it simultaneously reduced intergroup competition when wild resources were scarce.

The JI increased shortly thereafter in the Late Woodland to Mississippian periods, peaking about a millennium ago when cultigen use was greatest (Figs. 1 and 2). Dietary and population changes were accompanied by an increase in intergroup conflict, as indicated by skeletal trauma and, increasingly from the 11th century CE onward, palisades surrounding villages (54, 57). By the early years of the first millennium CE, some of the most heavily populated and powerful societies to have existed in eastern North America were firmly established in resource-rich river valleys (42, 56, 63). Aggregations of settlements increased local population densities and hence pressure on nearby resources. Greater intergroup conflict meant correspondingly fewer opportunities to disperse during lean times, despite expanses of uninhabited land between pockets of population. Insufficient alternative foods to ameliorate periods of hunger and higher unpredictable losses of life from attacks that disrupted essential household activities are consistent with higher age-independent mortality. Conflict could result in numerous deaths, with up a third of all adults being killed in attacks on one particularly hard-hit village dating to ca. 1300 CE (64). Diseases also contributed, directly or indirectly, to many deaths. Among them were tuberculosis and a treponemal infection, both of which were chronic, debilitating conditions suffered by many members of some communities (65–69).

After several centuries, the JI declined. That happened during a period of intergroup conflict coupled with group movement, the dissolution of formerly powerful societies, and population decline (42, 54, 56, 57). By 1500 CE, much of the midcontinent was depopulated, and inhabited places were more widely dispersed than they had been only a few centuries earlier (26). Despite considerable intergroup conflict, the decline in age-independent mortality raises the possibility that this change was primarily driven by altered subsistence practices and reduced local pressure on primary and alternative sources of food. The plant data indicate diets were more diverse than they were just a few centuries earlier, making them more resilient to resource shortfalls that inevitably occur.

The shifts in diet and mortality took place during a period of population growth, although available data from eight states are too coarse to provide temporal resolution comparable to the archaeobotanical and skeletal remains (Fig. 2). Growth rates increased for more than 2 millennia leading up to, and including, the widespread adoption of the EAC. An initial rise in growth rates coincided with the appearance of several native domesticates, indicative of human involvement in the life cycles of these weedy species, such as scattering seeds across organic-rich encampment soil and tending the plants as needed (9, 10, 43). That was when quasi-sedentary hunter-gatherer societies were increasingly focused on spatially fixed and locally productive resources with a high reproductive potential. This transformation in ways of life is archaeologically most visible as massive shell and midden heaps in some places. But quantitatively speaking, the EAC plants are poorly represented in archaeobotanical samples from the hunter-gatherer sites. It was not until well afterward, around 2 millennia ago, that many samples include numerous EAC plant remains.

The eventual shift to maize and a rise in age-independent mortality occurred when population growth slowed. The midcontinental population decline during the final centuries of the precontact period is largely masked in Fig. 2 by the inclusion of five states, out of a total of eight, that continued to be well populated into the 16th century.

Finer temporal controls on population growth rates, probably through compilations of radiocarbon dates, are needed to tie them to changes in age-independent mortality and subsistence practices. Nevertheless, it is clear that the long transition to native and introduced cultigens was generally accompanied by an increase in regional population size (42).

Regional Developments in Context

Understanding what occurred during the emergence of food-producing economies requires abundant archaeological data with reasonable temporal controls. Regions must be big enough to capture general tendencies but not so large that they conflate dramatically different cultural trajectories, obscuring general patterns and processes. Central tendencies are important because of the considerable variation attributable to actual cultural differences and how archaeological data are collected and reported.

With regard to the JI figures, previous studies generally arrayed samples in time according to years earlier or later than an agricultural sectioning point (1, 13, 41, 70–73). Doing so accommodates varied cultural trajectories, allowing the inclusion of numerous geographically and culturally diverse samples. But precisely when agriculture appeared in any particular area is open to interpretation. In the North American midcontinent, it might be when several native plants were first domesticated or perhaps a few thousand years later, when either the EAC or the IPs became well represented in archaeobotanical samples. Here we simply arranged samples in a temporal sequence, similar to work in the American Southwest (74).

Population-related information for the midcontinent falls in line with what has been previously reported from different data. Growth rates ranging from −0.006 to 0.07% for 500-y intervals estimated from site counts are consistent with 0.04 to 0.05% growth over many millennia estimated from radiocarbon probability distributions for North American foraging and early farming societies (29, 31). These figures represent only a small fraction of the growth rate range in *SI Appendix*, Fig. S1 (*SI Appendix*, section 1). Higher rates of long-term growth of 1% or more, as sometimes used for modeling purposes, are unrealistic for cemeteries containing skeletons that accumulated over many generations. Our JI estimates from the fitted curves correspond to age-independent (α_2) mortality of 0.006 to 0.021. They are within the 0.0 to 0.024 α_2 range reported for 20th-century hunter-gatherers and traditional subsistence agriculturalists (75). There is, therefore, no obvious reason to

dismiss the midcontinental population figures estimated from error-prone archaeological and skeletal data.

There are now enough JI analyses from different parts of the world to identify several long-term patterns in the human experience (1, 13, 41, 70–74). The JI curves for quasi-sedentary hunting-and-gathering societies—broadly considered a Mesolithic existence—are smoother compared to what is seen in later societies (1, 13, 41). However, data are relatively sparse, much like they are in Fig. 2. The appearance of the curves for these hunter-gatherer societies is likely an artifact of insufficient sampling. More interestingly, a low point in the JI is reached around the time of agriculture's emergence, as defined in various studies, to as much as a millennium earlier (1, 41, 70, 71, 73). That is consistent with the North American midcontinental samples, as long as agriculture's emergence is considered to be the widespread use of the EAC, not the initial appearance of native domesticates or the adoption of maize. Following agriculture's emergence, regardless of how it is identified, there is an increase in the JI in skeletal samples from several parts of the world (1, 13, 41, 70–74). The midcontinental skeletons reinforce the possibility that a low point followed by an increase in age-independent mortality was a common feature of the move toward agricultural economies, transcending great differences in specific cultural contexts.

Interpreted as primarily an age-independent mortality indicator, an increase in the JI for many groups worldwide during the transition to agriculture was presumably an outcome of more people living together for longer periods of time. Compact settlements resulted in contaminated food, soil, and water, and they facilitated the direct interpersonal transmission of pathogens. During resource shortfalls, the effectiveness of alternative food-acquisition strategies based on widely distributed plants or animals was reduced wherever settlements were clustered together, elevating local population densities. Tensions among groups over scarce resources could turn foraging across large areas into a hazardous undertaking. While the relative importance of such challenges must have differed from one cultural setting to another, they were all related to a shift toward agricultural ways of life.

Age-independent mortality then drops in some studies (13, 70, 72, 74). Present data are not sufficiently robust to say if a rise and fall in the JI relatively early in the transition to agricultural economies was a common feature of human existence or why it might have occurred. But in the North American midcontinent, the decline in the JI took place during a period of population reduction when settlement clusters became more widely distributed and the dietary contribution of cultigens declined.

Within the context of the JI reflecting fertility, the JI's decline has been interpreted as indicating higher mortality stemming from density-dependent stresses on the new agricultural way of life (13). People had begun to experience Barrett and colleagues' (76) "first epidemiologic transition." Overall mortality increased as a counterweight to fertility; if it did not, populations would have risen to impossible levels. Here, however, such a fertility and mortality sequence is unnecessary. Age-independent mortality, not fertility, is seen as having the greatest effect on the JI for the kinds of societies archaeologists commonly study. This component of mortality dampens the effect of increased fertility that could occur in situations where sedentary life came to dominate human existence.

In the North American midcontinent, the population declined several centuries after the shift to a maize-based subsistence system (26, 57). A reduction in population also took place in Europe following the adoption of agriculture, as indicated by compilations of numerous radiocarbon dates (27, 70). The reasons behind such decreases have yet to be clearly identified. Nevertheless, in the midcontinent, they accompanied a combination of climatic events, warfare leading to great losses of life that interfered with essential survival tasks, group movement and whatever disruptions it entailed, and factional competition within societies.

Conclusion

The usefulness of Bocquet-Appel's (13) JI is illustrated through skeletal remains from an archaeologically well-known region, but the interpretation of this demographic indicator departs from previous studies. The JI is more responsive to age-independent mortality than fertility and population growth in archaeological contexts.

Juxtaposing skeletal and dietary indicators arrayed by time, as is done here, clarifies what occurred during the transition to agricultural economies. That is particularly important in the North American midcontinent, where the long transition to more intensive forms of food production took place in a stepwise fashion. It was not a gradual process involving slow incremental changes.

Much like in other studies, there was an initial uptick in JI values in the midcontinent when people shifted to agricultural systems. Settlement size, compactness, and duration changed, leading to a greater disease load. Intergroup conflict sometimes resulted in considerable mortality that would have diminished the productive and reproductive capacity of communities. Such shifts in what people experienced must have occurred elsewhere in the world, where the JI also increased during the transition to agricultural economies.

Age-independent mortality in the midcontinent subsequently declined, which is also seen in groups elsewhere. For the people of the midcontinent, conflict continued to be an important aspect of life, so a drop in age-independent mortality was likely related to reduced pressure on resources in the immediate environs of settlements. A decline in the overall population and more diverse diets contributed to subsistence strategies that were more resilient to resource shortfalls. The changes were sufficient to result in a shift in mortality patterns captured by the JI. What occurred in other parts of the world where the JI also dropped must be explained in terms of regional cultural developments. It is encouraging that simple archaeological indictors compiled from existing data can be used to monitor socioeconomic and demographic change over great periods of time.

Materials and Methods

Skeletal and archaeobotanical data were collected from published sources (*SI Appendix*, sections 2 and 3). Skeletons were excavated from 54 sites. Archaeobotanical remains came from flotation samples associated with 305 cultural components; many sites had more than one occupational component. Of this total, 292 included EAC, IPs, or both. Site totals from eight states in the eastern United States, including several beyond the midcontinent, were reworked from previously used data (42, figure 13).

Trends over time in age-independent mortality were monitored using Bocquet-Appel's (13) JI. Commonly interpreted as a measure of fertility, the JI is more responsive to the age-independent (α_2) component of the Siler model (36, 37) (*SI Appendix*, section 1). Population growth at half-millennium intervals was approximated through counts of archaeological sites. Sites were allocated to those intervals using state site-file classifications, often region-specific phases. Change in subsistence practices was measured using two proportions: the cultigens in archaeobotanical samples, (EAC + IPs)/(EAC + IPs + nuts), and the representation of maize and beans in samples of cultigens, IPs/(EAC + IPs). Nuts

serve as an indicator of wild plants because they dominate that fraction of archaeobotanical samples.

Loess curves were fitted to skeletal and archaeobotanical data using R 4.2.0 (77) and ggplot2 3.3.6 (78). Samples were weighted by size, and spans of 0.62 and 0.6 smoothed curves for skeletons and plants, respectively. The span lengths avoided overfitting while retaining general tendencies in the data. For presentation

purposes, values slightly less than zero produced through loess smoothing were set at zero in Fig. 1. A loess curve with a span of 0.62 was fitted to the site count growth estimates.

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