PNAS SPECIAL FEATURE: INTRODUCTION

The past 12,000 years of behavior, adaptation, population, and evolution shaped who we are today

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PNAS has a long history of presenting research results relating to human evolution, including numerous breakthroughs in paleoanthropology, especially as they pertain to the evolution of Pliocene–Pleistocene and early hominins. *PNAS* readers are far less familiar, however, with the remarkably dynamic record of biological change, adaptation, stressors, and circumstances that have altered the behavior and well-being of *Homo sapiens* over the course of the most recent 12,000 y of human evolution, one of the most dynamic periods of human adaptation and evolution and the remarkable challenges to health and wellbeing. Based on the study of human remains from Holocene settings and the associated contexts of diet, behavior, and lifestyle, this set of Perspectives and Research Articles provides readers with new and emerging insights into the human condition and what has shaped human biology, health, and lifestyle over the course of the last 10 or so millennia. This record makes clear that human evolution and biological change, adaptation, exposure to long-standing and newly emerging infectious diseases, population demography, and warfare have continued in important ways over the course of the last 10 millennia, leading to the conditions associated with overpopulation, undernutrition, violence, and other circumstances we face globally today.

Among the most impactful dietary and behavioral transitions in hominin evolution—along with the control of fire, use of tools, and hunting—was the shift from a subsistence strategy based on foraging for wild food resources to a lifeway fueled by the production and consumption of domesticated plants and animals. The shift from foraging to farming, beginning some 12,000 or so years ago, changed everything. Today, our foods are derived almost entirely from domesticated resources. Among other impacts, the reliance on domesticated resources fueled increasing global population and a shifting of human settlement from a mostly transitory to an exclusively sedentary existence. The transition from foraging to farming had, and will continue to have, profound implications for world health, growth and development, well-being, behavior, conflict, and virtually every aspect of our individual lives now and going forward. Dependence on domesticated resources for our diet and nutrition has had considerable influence on our evolution, health, and well-being as pertaining to exposure to long-existing and emerging novel pathogens, resource availability and quality of nutrition, and migration and mobility patterns (1, 2).

The Agricultural Transition

At various times and in various settings, the transition to and adoption of farming as a central element of resource acquisition has contributed to increased intra- and intercommunity and regional competition for resources, sometimes leading to outright violence and warfare, patterns of behavior that will continue well into the future of our planet. Bioarchaeology, the contextualized study of human remains from archaeological settings, has taken a lead role in documenting and interpreting the record of health, well-being, and lifestyle impacts on our lives today (3–5).

The earliest archaeological record of the transition from foraging to farming was in the Levant region of the Eastern Mediterranean basin beginning approximately 12,000 y ago (6). Across the world, the more than eight billion of us alive today are dependent on domesticated foods, both plants and animals. This dependence focuses heavily on domesticated plant carbohydrates, but with considerable variation in access to quality nutrition. In this regard, the world's three so-called superfoods—rice, wheat, and maize—fuel the majority of all human energy requirements today, especially where persons and communities have limited access to animal sources of protein.

The archaeological record documents the appearance of independent centers of plant and animal domestication first in Southwest Asia. However, domestication centers also developed in many other settings globally, including across Asia, Africa, New Guinea, North America, and South America (6–9). Early farmers sustained their dietary and nutritional needs from domesticated food sources, but only in part. That partial focus has long since ended so that virtually everyone across the globe relies heavily on farming-based food sources—both plants and animals—for their energy requirements and survival.

Many authorities view the transition from foraging to farming as a long process taking upward of several thousand years in some settings. However, in terms of the six or so million years of hominin evolution, the transition from foraging to farming is an eye-blink in time. By every measure, the agricultural transition and the accompanying onset of the Anthropocene have played central roles in shaping health and its challenges, increasing conflict and competition for territory, access to key foods and other resources, rising levels of infectious disease, behavioral adaptations

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Author contributions: C.S.L. wrote the paper.

The author declares no competing interest.

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Published January 17, 2023.

involving reduced physical activity and mobility, migration, permanent or near-permanent settlement, and the threat of or engagement in inter- and intracommunity violence and warfare (1, 10).

Contributors to this *PNAS* Special Feature present analyses of the bioarchaeological record and of the foraging to farming transition involving a growing commitment to, and full dependence on, farming (e.g., maize in the Western Hemisphere, wheat in Europe and Asia, and rice in Asia). This Special Feature focusses on bioarchaeology, a field pertaining to the contextualized, biocultural study of human remains from archaeological settings (11). This large and growing record provides the context for all our lives today, especially our lifestyle, health, and diet. The shift in foodways from ones based on hunted, gathered, or collected resources to those based on farming in such a brief span of time resulted in a pattern of insufficient nutrition and other significant health challenges owing to the kinds and quality of foods we eat (12).

The transition from nondomesticated to domesticated foods. shaped our past and present worlds beginning at the Pleistocene–Holocene transition during a period of dramatic warming globally and ecosystem change and including many independent centers that first arose in Southwest Asia and then in a range of centers globally (13). With the appearance of numerous domestication centers in Asia, Africa, and North and South America, farming spread rapidly and widely. By most measures—rising population size, appearance of new and growing population centers, challenging dietary transitions, and infectious disease exposure and increasing negative health outcomes—the agricultural transition and the accompanying onset of the Anthropocene have formed who we are in the twenty-first century. Recent and newly emerging analyses of the record of health, diet, biological relationships, migration patterns, dietary adaptations, activity, and lifestyle reveal that the growing commitment to, and dependence on, farming beginning at the Holocene–Pleistocene boundary was as impactful—if not more so—than any other dietary development or behavioral transition related to the food quest and acquisition of resources generally. In large measure, the last 10,000 to 12,000 y have had profound implications for who are today and in every part of our lives.

Domestication led to a transformation in the kinds of foods humans acquired involved fundamental changes, including a shift from broad dietary diversity to a reliance on, and commitment to nutritionally limited food staples, notably domesticated plant carbohydrates; food sources having reduced nutritional quality; and reduced access to animal sources of protein. Combined with origins and rise of social inequality, the increasing reliance on domesticated plant carbohydrates beginning at the Pleistocene–Holocene transition has resulted in today's striking reduction in access to adequate nutrition for most of the world's population, now at over eight billion persons. In addition to undernutrition, urban environments and greater interconnectivity of people have resulted in unprecedented challenges, predictably along social lines, from exposure to both long-standing and newly emerging pathogens that cause acute and chronic infectious diseases. The threat of such diseases was underscored globally via illness, disability, and loss of life associated with the 2020 coronavirus pandemic. It was just one of the viral infectious diseases that have emerged in the last several decades, and is a predictable outcome related to remarkable increases in population size and density, the growing number of large, settled communities, and intercontinental contact. These consequences are exacerbated by the impacts of global warming, also a long-term outcome of technological changes due in part to the use of fossil fuels that drive the agricultural industry globally. The development of new landscapes for the transmission of pathogenic microbes, conditions leading to inadequate diet and nutrition, and other challenges that began with early farming and permanent settlement at 10 or so millennia ago will continued unabated. In particular, the threat of emerging and reemerging infectious diseases is likely to dominate our lives for the foreseeable future.

This Special Feature underscores the central point that the transition from foraging to farming is a critically important period in the history of our species, a development underpinning the remarkable increase in global population from 10 million in the later Pleistocene (14) to the present-day eight billion. Largely fueled by shifting patterns in population fertility and mortality, once small, sedentary communities grew to large and densely crowded, farming-based settlements, especially with the eventual development of urban centers having thousands of individuals (10). This demographic transformation created the circumstances ideally suited for the evolution and transmission of pathogens, including but not limited to infectious diseases that have profoundly impacted societies globally up to the present day (e.g., tuberculosis, treponematosis, dental caries, periodontitis, malaria, leprosy, parasitic infections, and many others).

The links between population, health, and well-being for the last 12 millennia are based on an extensive and growing bioarchaeological record focusing on health, nutrition, and behavioral transformations in farming settings. Research programs and a rapidly expanding literature pertaining to many parts of the world describe and interpret the costs, consequences, and social and behavioral outcomes of the foraging-to-farming transition and food-production intensification. This record places humans in the larger context they play in transforming their environmental, health, and behavioral worlds, much of which has led to the profound challenges we face in the twenty-first century.

The Special Feature contributions focus on dietary and inadequate nutritional quality, resource inequality, conflict and warfare, climate change, population trends, demographic transitions, migration, mobility, and human biology. The research by biological anthropologists includes diverse investigations of ancient genomics and genetics, reconstruction of diet and ecology, and morphological variation as it pertains to growth and development and temporal shifts in disease and other circumstances. Building on earlier studies, the results of recent research are providing a growing understanding of both the adaptations and the costs in health and security associated with the transition from hunter-gatherer lifeways to farming.

This Special Feature

Over the course of the planning and development this Special Feature, all of us involved have been struck by the

remarkable challenges faced by past people. The world's challenges today derive in part from food choices dominated by domesticated plant carbohydrates and their products; diminishing access of quality diets; the emergence of, and exposure to, novel pathogens and evolution of long-existing pathogens; and an increasing frequency of epidemics and pandemics in the twenty-first century, such as those caused by the RNA viruses, including ebolaviruses, Zika virus, and especially the pandemic-causing SARS-CoV-2 viruses (15, 16). Although Ebola, Zika, and numerous other infectious diseases have caused dramatic health challenges globally, most thus far have not had the profoundly devastating outcomes as COVID-19, which resulted in illness in the tens of millions of infected individuals and millions of deaths globally (17). These circumstances and challenges pertaining to the last 10,000 y of human evolution and the environmental and economic stress associated with global warming, arable soil depletion, forest clearance, and a profoundly and remarkable population increase and rising density speak to the importance of sustainability, food availability, access to quality nutrition, and health going forward. The current growth rate is not the first time humans have grappled with the stresses of overpopulation. Indeed, the archaeological record shows the challenges of overly dense population centers regarding rise in infectious diseases and intracommunity and intercommunity conflict.

This Special Feature introduces the broad patterns of health and well-being based on the bioarchaeological record. In Perspective 1, Robbins Schug et al. (18) make the case that climate change and its impact on health and well-being extends far back into prehistory. Epidemiological evidence drawn from archaeological contexts reveals that communities responded to environmental challenges in diverse ways, with important implications for dietary sufficiency, disease ecology, migration, and interpersonal violence. Robbins Schug et al.'s discussion underscores the important point that social inequality and unequal access to resources is the biggest epidemiological threat in the face of climate change. Communities that had sufficient access to resources had less experience with violence than those with insufficient resources (19). Importantly, there is considerable community variation in the record of violence depending on the duration and severity of drought and the sociopolitical means of dealing with it.

Milner and Boldsen (20) address the dramatic rise in population over the course of the Holocene, a development tied to key dietary transitions associated with the foraging-to-farming transition that included a growing reliance on carbohydrate-rich domesticated plants (e.g., maize). In eastern North America, the long road to agriculture was a stepwise development accompanied by changes in age-dependent mortality. Their findings reveal a demographic signal matching other areas of the world at the time of newly emerging agricultural societies (21). Changes in demographic regimes linked to the kind of food sources available, primarily storable domesticated plants and other food products derived from farming. In short, population and subsistence histories are closely aligned.

A fundamental question about the origin of farming practices and languages, namely *Were agricultural practices spread via migration of early farmers who brought their languages and social and cultural practices, sharing them with the communities they encountered?* Alternatively, *did foraging communities adopt farming and languages from nearby farmers?* These questions, once unresolvable, are now tractable, via genetic analyses. In Perspective 2, Stoneking and collaborators (22) develop a broad genomic survey of Africa, Europe, Central and South Asia, East Asia and Mainland Southeast Asia, Island Southeast Asia and Oceania, and the Americas, documenting a complex picture of Holocene human dispersals. Although much remains to be learned, migration and dispersal analyses are becoming increasingly informed by large-scale genomic analyses.

Scaling down to a single setting, Çatalhöyük, a permanent Neolithic settlement housing some 5000 to 8000 persons at its peak occupation, is among the most comprehensively documented early farming communities in Western Asia (10). The setting marks the end of societies engaged in primarily hunting-and-gathering and living in small impermanent communities and a shift to settlements involving significant growth and permanent residency. These communities were inhabited by hundreds to thousands of individuals who focused on farming—wheat, barley, and rye—as dietary mainstays. Pearson et al. (23) address mechanisms associated with kinship in these early farming contexts. Their analysis of strontium and oxygen isotopes from tooth enamel of early farmers associated with the earlier community of Pınarbaşı and later communities of Boncuklu and Çatalhöyük reveals that Çatalhöyük is the only settlement to show the presence of nonlocals. These findings point to continuity and diversity in kinship, especially regarding unique social and biological kinship identities, laying the foundation for kinship and community organization in later societies of western Asia.

Lewis et al. (24) make the compelling case that changes in settlement involved population increase and density, thereby creating the ideal macro- and microecological conditions for the origins and spread of opportunistic pathogens. These observations for past populations are now well documented for large, densely crowded, early farming communities (3). Especially important are the common zoonotic diseases that can be transmitted from vertebrate animals to people. Owing to the climate stability, warm temperatures, loss of dietary breadth, and a suite of other vulnerabilities in the Holocene, Lewis et al. identify key elements and the context for an increased disease burden in early settled communities. The bioarchaeology of infectious disease provides us with an important picture of morbidity and health crises, especially those relating to chronic conditions in early farming communities.

Remarkable increases in population and intercommunity competition for access to arable land by early farmers are now well documented for a wide range of settings globally. Yet rarely is there the opportunity to meld context with outcomes in a part of the world where the investigation of warfare has depth and breadth. Neolithic Northwestern Europe is among the most comprehensively documented settings of conflict that involved multiple groups competing for arable land and other resources. The emergence of animal and plant domestication, sedentism, population increase, and competition for arable land and other resources presents us with the context for the rise of interpersonal violence and warfare in Europe. Some 10% of

individuals documented by Fibiger et al. (25) died from traumatic injuries in early farming communities across the western and central Europe. Their analysis reveals that violence in Neolithic Europe was endemic and was scaling upward, resulting in patterns of warfare leading to increasing numbers of deaths.

Although crop production was central to acquisition of food, dairying—and especially milk production—was a key element of domestication in Europe, Asia, and Africa. As with all other circumstances associated with the foraging to farming transition, there was considerable regional biological variation. Stock and collaborators (26) address the impact of dairying via their analysis of human stature and body mass based on an unprecedented number of individuals and sites encompassing seven regions globally where domestication involved dairying and crop production. Presence of whey protein in dental calculus (27) shows the earliest evidence of milk consumption at 5,000 yBP in northern Europe. It denotes lactase persistence, the genetic variant that identifies adaptation to consumption of milk as a protein source.

Conclusions

In evolutionary terms, the transition at the Pleistocene–Holocene boundary was extraordinary, especially in consideration of the beginning of a fundamental shift in dietary focus and the downstream effects of diets based on domesticated plants and animals. The transition provided the context for a remarkable increase in population. However, the costs for that success—elevated levels infectious diseases, undernutrition, and conflict—are still with us today. Our species will continue to adapt, to develop strategies for success, and to mitigate challenges. That is what we do. Once we began the shift to and intensification of farming, the remarkable changes seen in humans became critically important developments in recent human evolution. In view of conditions today, including climate change, overpopulation, and the rise in prevalence of infectious diseases, both old and newly emerging, it should come as no surprise that dependence on a few staple crops and shift to sedentary behavior will be with us for the foreseeable future. They are, after all, a legacy of our past, and forming and sharing of the dietary framework, behavioral patterns, and outcomes in health and well-being for all eight billion of us that occupy the world today.

ACKNOWLEDGMENTS. All of us involved in this Special Feature are indebted to Owen Lovejoy for his support in the preparation and submission of research articles and perspectives. We are indebted to the reviewers for their recommendations. Their input was enormously helpful to both the authors and to me in my role as editor.

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