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Dispatch

Human evolution: The unsealed fate of foragers and farmers

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It is commonly thought that the spread of agriculture and farmers led to the decline of hunter-gatherer populations. A new study found that the demographic responses of Ethiopian foragers to this major cultural transition have been more diverse than anticipated.

Until approximately 12,000 years ago, human societies relied solely on wild plant and animal food for their subsistence. The persistence of hunter-gatherers to this day demonstrates that this subsistence strategy has long been a successful adaptation to many different ecosystems. Still, a century of archaeological research has revealed that human subsistence patterns shifted massively from foraging to agriculture and pastoralism within a few millennia, in nearly all continents¹. It is commonly accepted that this major transition came about because species domestication enabled effective food production, but how this transition occurred remains unclear. It has been proposed that foraging societies were simply replaced by farmers, owing to demographic and technological advantages (the ‘migrationist’ theory²), or, conversely, that they adopted the way of life of neighboring farming communities (the ‘diffusionist’ theory). Recent advances in ancient genomics have enabled researchers to shed new light on this question, providing a more nuanced picture: while large-scale migrations of farmers played a central role in the diffusion of material cultures and languages, they often resulted in admixture with hunter-gatherers, rather than a complete population replacement³. Yet, these findings mostly pertain to Europe, where the archaeological records are dense and well-characterized. Furthermore, 3–5% of human societies

continue to depend on hunting and gathering⁴, but little is known about how these populations have persisted as hunter-gatherers. In a new study in this issue of *Current Biology*, Shyamalika Gopalan, Richard Berl and colleagues⁵ examine the genomic diversity of foraging and farming societies from Ethiopia to uncover the various responses of hunter-gatherers to the rise of agriculture and pastoralism.

How the Neolithic transition has affected human cultural diversity and demography is a long-standing question. In April 1966, during the influential conference *Man the hunter*, a consensus emerged among scholars that studying contemporary foraging societies could provide clues on how humans lived before the emergence of agriculture. This motivated a burst of research on the subsistence strategies and demography of extant hunter-gatherers. These studies highlighted that foragers make use of very diverse hunting and gathering techniques and wild food resources⁶. Furthermore, socio-demographic data showed that what characterizes hunter-gatherers is not only their subsistence based on foraging, but also a social organization that typically consists of small, mobile groups of 15–30 individuals⁷. These findings led researchers to hypothesize that the size of foraging groups is kept small to prevent exhaustion of food resources. The growth rate of mobile, foraging populations is thus expected to be lower than that of sedentary, farming populations, which produce more stable food supplies. Nevertheless, this hypothesis could hardly be tested, as multigenerational demographic data and archaeological records are scarce or absent in most regions inhabited by hunter-gatherers. Over the last decade, fueled by the advent of improved DNA typing technologies, population genetics has offered an attractive alternative approach to reconstruct past human demography. Using a limited number of genetic markers, seminal studies have shown that most foraging groups have experienced population decline while farming populations grew⁸⁻¹¹, implying that subsistence patterns have affected human demography. However, how population sizes changed during the Holocene — when the transition to agricultural food production occurred — has remained uncertain, owing to methodological limitations and the sparsity of the genetic data used.

By generating genome-wide data and assessing more than a million genetic variants in five foraging and farming groups from Ethiopia, Gopalan, Berl and colleagues⁵ are now well positioned to shed new light on the impact of modes of subsistence on population size. Ethiopia, the largest country in the Horn of Africa, is peopled by more than 90 ethnic groups, which speak divergent languages and practice diverse subsistence strategies. The region is ideal to study the fate of hunter-gatherers following the emergence of farming, as agro-pastoralism emerged in Ethiopia relatively recently — by only the third millennium before present¹² — and several Ethiopian populations are still active hunter-gatherers, including the Ongota, the Waata, the Manjo and the Chabu (Figure 1). Furthermore, the first ancient African genome was obtained for ‘Bayira’, an adult male excavated in the Mota Cave (Ethiopia) and dated to 4,000–4,500 years before present, offering a glimpse of what the gene pool of Ethiopian hunter-gatherers was like before the rise of farming^{12,13}. Gopalan, Berl and colleagues⁵ generated genomic data from the Chabu hunter-gatherers and the Majang, the Shekkacho, the Bench and the Sheko, who are neighboring groups who adopted horticulture at different periods. They also analyzed jointly other East African groups with different modes of subsistence, including the Aari, the Wolayta, the Hadza and the Sandawe, and used a recent method, IBDNe, to accurately estimate the effective sizes of all populations during the last two millennia. This method leverages dense genome-wide data and the quantity of long genomic segments that are identical by descent, to infer the recent demographic history of a population¹⁴. At odds with previous studies, Gopalan, Berl and colleagues⁵ find that the correlation between subsistence strategy and demographic history is not universal. Specifically, the size of some agriculturalist populations has recently declined, while closely related societies with similar subsistence patterns have had distinctive demographic trajectories.

The authors report evidence for at least three demographic responses associated with the spread of agriculture and pastoralism in Eastern Africa. First, foraging societies have all experienced a population collapse, as previously reported⁸⁻¹¹. The Chabu, who are related to the ancient Bayira individual and are considered as the most active foragers in Ethiopia¹⁵, have abruptly declined over the last millennium, possibly because

they have faced a drastic reduction of the forested lands they have inhabited traditionally. Other African hunter-gatherer societies have probably experienced the same demographic decline due to a reduced geographic range, including the Hadza from Tanzania⁵ and the Batwa from Uganda¹⁶. Importantly, all these populations show signatures of recent admixture with neighboring agriculturalists, despite their relative geographic isolation.

Second, several Southwestern Ethiopian populations have adopted the way of life of neighboring farming communities and have experienced net growth, including the Gumuz, the Aari Cultivators, the Shekkacho and the Wolayta, which is again in line with previous observations. However, the present study also shows that other groups that have shifted to horticulture or iron working have experienced a population decline. In particular, the population size of the Majang, the Sandawe and the Aari Blacksmiths has decreased over the past 1,500 years. The Majang and the Sandawe practice small-scale cultivation and agro-pastoralism, respectively, whereas the Aari Blacksmiths are craftspeople that have entered into a tight socio-economic relationship with neighboring Aari Cultivators. Intriguingly, the Majang share strong genetic and cultural similarities with the Gumuz but have experienced a different demographic history. Gopalan, Berl and colleagues⁵ suggest that the Majang have adopted horticulture later than the Gumuz, or that other factors, including ecological differences, have affected their population size. Together, these findings question the common view that only foraging groups have declined during the rise of farming and pastoralism.

The new study by Gopalan, Berl and colleagues⁵ well illustrates the diverse responses of foraging societies to the cultural and demographic changes associated with the spread of agriculture and pastoralism. Several groups have persisted as hunter-gatherers, demonstrating their great resilience; yet, they have all systematically declined over the last centuries because of increasing pressures from surrounding farmers, forced movements to unproductive lands or ecological factors that are yet to be determined. A first important implication of these findings is that the present-day demography of African foragers is not indicative of past human demography and, thus,

past subsistence strategies. In addition, these results imply that, only a few centuries ago, Eastern African hunter-gatherers were numerous and demographically successful. The high genetic diversity of extant Central and South African hunter-gatherers also suggests that these groups were formerly large meta-populations that became reduced during the Holocene^{17,18}. In agreement with this hypothesis, an archaeogenetic study showed that the Eastern African Hadza, the Southern African Khoe-San and ancient Southeastern African foragers once formed a continuum of related populations¹⁹. However, the latter group did not contribute to the gene pool of contemporary populations, implying that the spread of farmers in Africa also involved complete replacement of local populations. Collectively, genetic studies, including that by Gopalan, Berl and colleagues⁵, increasingly support the notion that human demographic responses to major cultural transitions do not follow simple rules.

Declaration of Interests

The author declares no competing interests.



Figure 1. Ethiopian hunter-gatherers.

Chabu foragers from southwestern Ethiopia (Gifor site, December 2010; photo: Kiebe Tsehay)

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