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The shrinking human gut microbiome

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Mammals harbor complex assemblages of gut bacteria that are deeply integrated with their hosts' digestive, immune, and neuroendocrine systems. Recent work has revealed that there has been a substantial loss of gut bacterial diversity from humans since the divergence of humans and chimpanzees. This bacterial depauperation began in humanity's ancient evolutionary past and has accelerated in recent years with the advent of modern lifestyles. Today, humans living in industrialized societies harbor the lowest levels of gut bacterial diversity of any primate for which metagenomic data are available, a condition that may increase risk of infections, autoimmune disorders, and metabolic syndrome. Some missing gut bacteria may remain within under-sampled human populations, whereas others may be globally extinct and unrecoverable.

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Introduction

A typical human harbors on the order of 10^{13} bacterial cells in the large intestine [1]. This gut microbiota, which can contain over a thousand species, is deeply integrated with virtually every tissue and organ system in the body. Gut bacteria process difficult to digest components of the diet, promote angiogenesis in the intestine [2], train the immune system [3], regulate metabolism [4], and even influence moods and behaviors [5].

Humans' intimate relationships with gut bacteria likely reflect a long history of coevolution, wherein host and symbiont lineages have acted as selective forces on one another over millions of years. Recent work has shown that some of the most prevalent bacteria in the human gut are descended from ancestral symbionts that have

persisted within the human lineage since before the divergence of humans and gorillas [6]. The maintenance of gut bacterial lineages within host lineages over evolutionary timescales is consistent with the possibility that these symbioses have been conserved by selection. Under this view, disruption of the gut microbiota is expected to negatively impact human health.

Here, I summarize current understanding of the changes in the composition of the gut microbiota that occurred over the course of human evolution. In particular, I review recent evidence that humans have experienced a massive loss of gut bacterial diversity since diverging from chimpanzees. I discuss the timeline of this gut bacterial depauperation, the hypothesized causes, and the potential consequences for human health.

Ancient losses of gut bacterial diversity

Humans diverged from chimpanzees over six million years ago and have since undergone myriad phenotypic changes. One transition that came to distinguish Homo from Pan was increased consumption of animals by ancestral hominins. Evidence of persistent hominin carnivory has been reported from archaeological remains dating back to the first half of the Pleistocene ~2 million years ago [7]. Over the course of human evolution, the dietary shift away from plant-based foods and towards animal fat and protein has led to a reorganization of gut morphology as well as substantial changes in the bacterial composition of the gut microbiota.

Decreased reliance on dietary fiber and increased intake of animal fats and proteins during human evolution led to a reduction in the size of the large intestine. In the Great Apes, the large intestine composes over half of the total intestinal volume while the small intestine constitutes approximately one fourth [8]. In humans, these proportions are inverted, with the large intestine composing one fifth of the total intestinal volume and the small intestine constituting approximately 60% [8]. Across mammals, the ratio of small and large intestinal volumes differentiates carnivores and herbivores, with carnivore guts consisting of relatively larger small intestines and relatively smaller large intestines compared to herbivores [8]. Together, these observations suggest that the morphology of the human gut has become adapted to a meat-based diet since the divergence of humans and chimpanzees.

Coincident with a reduction in the volume of the colon, humans have experienced a substantial reduction in bacterial richness (*i.e.*, alpha diversity) within the gut microbiota since diverging from chimpanzees.

Comparisons of the gut microbiotas of humans and the African apes, enabled by high-throughput sequencing of 16S rRNA genes present in fecal samples, have revealed that individual humans, on average, harbor fewer phyla, classes, orders, families, genera, and species of gut bacteria than do individual chimpanzees, bonobos, or gorillas [9[•]]. This trend is recapitulated across a diversity of human populations representing a range of lifestyles, including Amerindians of the Amazon rainforest in Venezuela, rural Malawians, and urban Americans [9[•]].

The ancestral decreases in gut bacterial diversity within the human lineage are consistent with the reductions in dietary fiber and increases in the intake of animal fats and proteins that occurred during human evolution. Across mammals, carnivores tend to house the lowest levels of gut bacterial species richness per host, whereas herbivores harbor the highest [10]. Moreover, many of the bacteria that have decreased in relative abundance within the human gut microbiota are known to digest complex plant polysaccharides. For example, the relative abundance of *Fibrobacter*, a genus named for its fibrolytic activity, is over fivefold lower within the gut microbiotas of humans, regardless of lifestyle, relative to within the gut microbiotas of African apes [9[•]]. Conversely, the few bacteria taxa whose relative abundances have increased within human gut microbiotas include genera that are positively associated with the degree of meat-eating within human populations (*e.g.*, *Bacteroides*) [9[•],11].

Modern lifestyles dwindle gut microbiomes

The dietary transition toward carnivory in the early evolutionary history of hominins has been hypothesized to have contributed to the evolution of larger brains and improved cognition [12]. Subsequent to these neurological enhancements, some of the most conspicuous differences between humans and other apes have arisen as a consequence of human culture. Approximately 12 000 years ago, at the dawn of the Holocene, multiple human populations around the world simultaneously shifted from hunter–gatherer lifestyles to settled, agricultural societies [13]. This Neolithic Revolution began a prolonged period of rapid cultural evolution that has accelerated within industrial and post-industrial societies over the last ~300 years. Extant variation in lifestyle practices of human populations around the world afford an opportunity to evaluate how these cultural transitions have impacted the composition of the human gut microbiota.

Available data suggest that transitions from hunter–gatherer to agricultural lifestyles have led to shifts in the relative abundances of gut bacterial taxa but little or no change in gut bacterial richness. Gomez *et al.* [14^{••}] compared the gut microbiotas of two coexisting human populations residing within the Central African Republic: the BaAka, who maintain a hunter–gatherer lifestyle, and the Bantu, who have adopted an agricultural lifestyle.

Consistent with the dietary differences between these populations, the BaAka hunter–gatherers harbored higher levels of bacteria capable of amino-acid and vitamin metabolism, whereas the Bantu agriculturalists harbored higher levels of bacteria capable of carbohydrate and xenobiotic metabolism. However, the authors detected no significant differences in per-host bacterial species richness between the gut microbiotas of the two populations. Similarly, Obregon-Tito *et al.* [15] and Morton *et al.* [16[•]] compared the gut microbiotas of hunter–gatherer and traditional agriculturalist populations in Peru and Cameroon, revealing compositional differences between the gut microbiotas of host populations consistent with dietary differences, but no differences in per-host bacterial species richness.

In contrast to hunter–gatherer to agricultural transitions, adoptions of industrial and post-industrial lifestyles have led to massive reductions in bacterial richness within human gut microbiotas. Individuals living in urban centers in the United States harbor fewer gut bacterial species on average than do individuals living more traditional lifestyles in Malawi [17], Venezuela [17,18], Peru [15], and Papua New Guinea [19]; the gut microbiotas of urban Nicobarese people are less species-rich than are the gut microbiotas of Nicobarese living more traditional lifestyles [20]; the gut microbiotas of urban Italians are less species-rich than are the gut microbiotas of Hadza hunter gatherers [21] and display altered functional and resistome profiles [22]; the gut microbiotas of children living in urban Italy are less species-rich than are the gut microbiotas of children living more traditional lifestyles in Burkina Faso [23]; gut bacterial loads are higher in rural Africans relative to African Americans [24]; the gut microbiotas of urban Russians appear to be missing functional pathways associated with Gram-positive Firmicutes relative to the gut microbiotas of rural Russians [25]; and the gut microbiotas of Han Chinese are less diverse than are the gut microbiotas of Tibetans and Mongolians living traditional lifestyles [26,27]. High-throughput sequencing of fecal samples retrieved from archaeological contexts (*i.e.*, coprolites) dating between 1400 to 8000 years before present further corroborate the view that the gut microbiotas of industrialized populations have deviated substantially from the ancestral state [28]. The compositional profiles of the bacterial communities preserved within these ancient fecal samples more closely resemble the gut microbiotas of extant populations following traditional lifestyles than they do the gut microbiotas of extant industrialized populations [28].

Industrialized and traditional lifestyles differ in many respects, confounding the identification of the specific practices that have led to decreases in gut bacterial diversity within industrialized societies. One potential cause is the rise of food processing and the corresponding reductions in the intake of dietary fiber in favor of simple

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