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Gut Microbial Intersections with Human Ecology and Evolution

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Abstract

Although microbiome science is relatively young, our knowledge of human-microbiome interactions is growing rapidly and has already begun to transform our understanding of human ecology and evolution. Here we summarize our current understanding of three-way interactions between the gut microbiota, human ecology, and human evolution. We review the factors driving microbiome variation within and between individuals and populations, as well as comparative data from nonhuman primates that allow a more direct examination of microbial relationships with host ecology and evolution. Collectively, these data sets can help illuminate generalizable principles governing host-microbiome-environment interactions, the processes contributing to bidirectional influences between the human gut microbiota and the human ecological niche, and past changes in the human microbiome that may have harbored consequences for human adaptation. Developing richer insight into host-microbiome-environment interactions will ultimately broaden our view of human biology and its response to changing environments.

INTRODUCTION

Microbiota: a community of microorganisms

Microbiome: the genetic content and products of a community of microorganisms

Over the past two decades, it has become clear that the microbial community in and on the human body functions akin to an organ. This community, known as the microbiota, interacts with multiple body processes and systems, affecting metabolism, immunity, and behavior in myriad ways (Al Nabhani & Eberl 2020, Carmody & Bisanz 2023, Cryan et al. 2019, Pronovost & Hsiao 2019, Visconti et al. 2019). While some components of the microbiota are passed from parents to offspring, and can therefore be considered heritable, environmental factors such as diet, social networks, and hygiene practices also strongly shape the microbiota (Blaser 2016, David et al. 2014, Dominguez Bello et al. 2018, Korpela et al. 2018). As a result, the microbiota is considered a key mediator of host responses to environmental change and is likely a contributor to patterns of human ecology and evolution. However, research on the human microbiota to date has largely been clinical in nature, and important gaps remain in our knowledge that preclude a robust understanding of microbial contributions to human ecology and evolution. For example, it remains unclear which human traits are more strongly influenced by the human genome versus the human microbiota and the extent to which human genomic and microbiome content complement or conflict with each other. Nevertheless, the vast amount of existing microbiome data from humans and nonhuman primates provides an important starting point for understanding these complex relationships.

Here, we outline a broad framework for integrating the human microbiota into current perspectives on human ecology and evolution. Although microbes are found all over the human body, we focus primarily on the gut microbiota, given that it is the richest in both number and taxonomic diversity and is currently the most well-studied human-associated microbial community. We begin by exploring patterns of host-microbiome variation in modern human populations and the factors that drive it. We then describe current understanding of how the human microbiome has changed over evolutionary history and the processes that may have contributed to this change. Next, we leverage data from nonhuman primates to investigate how the gut microbiota can influence host ecology and evolution. Finally, we assess how well host-microbiota relationships identified in nonhuman primates are likely to translate to humans. In addition to summarizing the state of the field, our hope is that this review highlights key unanswered questions, contributes to the generation of new testable hypotheses, and encourages ongoing proliferation of research in this area.

GLOBAL VARIATION IN THE MODERN HUMAN MICROBIOME

There is no single human microbiome. Rather, the human gut microbiome varies substantially across populations, across individuals within populations, and within individuals across time (**Figure 1**), driven by factors including age (Yatsunenko et al. 2012), genetics (Bonder et al. 2016, Goodrich et al. 2016, Suzuki & Ley 2020), diet on long-term (De Filippo et al. 2010) and short-term (David et al. 2014) timescales, and broader correlates of lifestyle along an industrialization gradient, such as sanitation, access to medical care, antibiotic use, rates of cesarean section (c-section) births, physical activity, and exposure to environmental microbes (Blaser 2016, Dominguez Bello et al. 2018, Jha et al. 2018, Sonnenburg & Sonnenburg 2019a). Studies of immigration (Vangay et al. 2018), genetic variation within lifestyle cohorts (Rothschild et al. 2018), and meta-analyses of microbiomes sampled across populations (Smits et al. 2017) suggest that environmental factors generally play a larger role in shaping the human gut microbiome than do intrinsic host factors such as genetic background. Indeed, the human gut microbiome exhibits broadscale patterning along a primary axis explained by lifestyle and a secondary axis explained mostly by age (Smits et al. 2017). Nevertheless, specific genetic signatures such as those conferring lactase persistence have been found to shape the gut microbiome in predictable ways

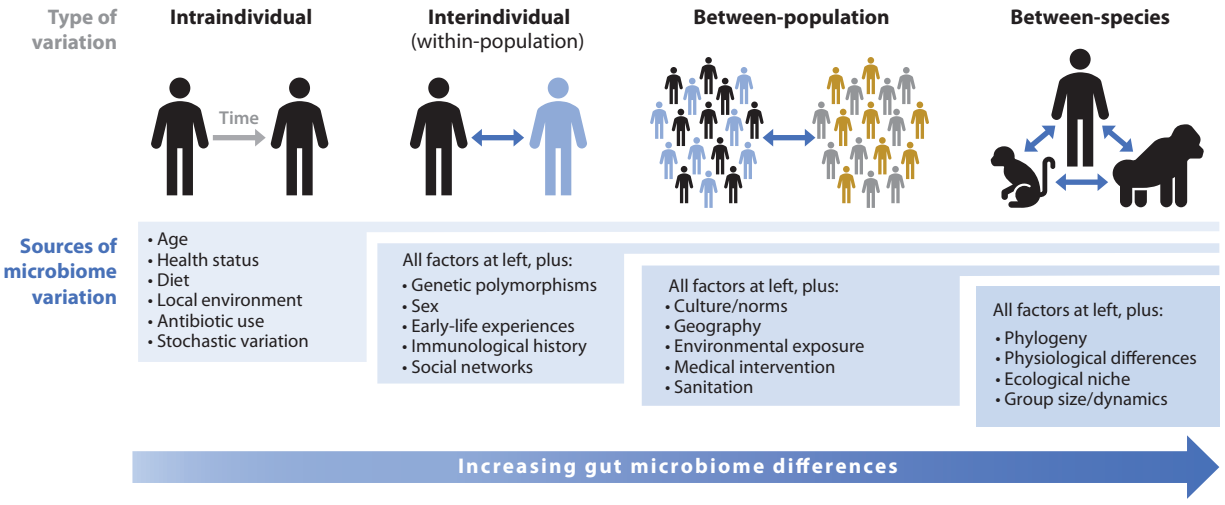

Figure 1

Sources of gut microbiome variation within and between individuals, populations, and species. Variation among samples (also known as beta-diversity) generally increases from left to right, although there may be specific circumstances (e.g., active infection, post-antibiotics, recent immigration, local ecological convergence between species) where variation can occasionally be larger within than between individuals or populations or species. Examples of this dynamic include observations that seasonal variation in the gut microbiome can eclipse average interindividual variation (Amato et al. 2015, Smits et al. 2017) and that gut microbiome variation between nonindustrialized and industrialized human populations can exceed that between humans and chimpanzees (Moeller et al. 2014, Reese et al. 2021a). The gray arrow represents the passage of time. The blue arrows represent contrasts in the gut microbiome between individuals or populations or species.

(Blekhman et al. 2015, Bonder et al. 2016, Kato et al. 2018, Suzuki & Ley 2020). Moreover, heritable taxa may have important phenotypic effects. For instance, twin cohort studies have found the bacterial family Christensenellaceae to be highly heritable and negatively correlated with body mass index (BMI) (Goodrich et al. 2014, 2016). Murine gnotobiotic recipients of an obese-associated microbiome gained less weight when *Christensenella* was added to the community prior to transplant, suggesting a causal effect of this taxon on host metabolic phenotype (Goodrich et al. 2014). Heritability of human phenotype-amending microbes that vary across hosts raises the intriguing still-untested possibility that some signals of natural selection on humans may be encoded in the microbial metagenome.

Interindividual variation in the human microbiome arises due to a complex interplay of environment-driven and host-driven influences beginning early in life. Researchers generally believe that human infants are colonized at birth (de Goffau et al. 2019). Initial seeding of the microbiome varies based on birth mode, with infants born vaginally colonized primarily by vaginal and gut microbes and infants born via c-section colonized primarily by skin microbes (Chu et al. 2017, Dominguez-Bello et al. 2010). While early colonizers in any ecosystem are predicted to have advantages in filling and modeling available niches, it remains unclear whether these initial differences in the gut microbiome contribute to lifelong phenotypes, as compositional differences between infants born vaginally versus by c-section appear to normalize early in childhood (Chu et al. 2017, Roswall et al. 2021). Nevertheless, even short-term gut microbial differences that resolve might influence development. For instance, short-term administration of antibiotics in early life can promote adult obesity in mice despite the microbiomes of treated and control individuals growing indistinguishable by four weeks of age (Cox et al. 2014). Moreover, microbial influences on the host could begin even prior to colonization through in utero exposure to

Gnotobiotic: germ-free or colonized with a known microbial community

Microbial metagenome: the combined genomes of multiple microbial taxa

Niche: the local environment and interactions with other organisms, which influence an organism's ability to thrive in a given ecosystem

microbial products. Remarkably, in mice, short-chain fatty acids (SCFAs) derived from the maternal gut microbiome have been shown to cross the placental barrier and shape the development of neural, intestinal, and pancreatic tissue, with the result that embryos exposed to SCFAs exhibit protection as adults against diet-induced obesity (Kimura et al. 2020). Whether vertical transmission enables intergenerational influences of the gut microbiome, which (if any) microbial influences on the human phenotype occur prior to birth, and how early embryonic and neonatal conditions predispose individuals toward particular gut microbial signatures remain important, unanswered questions.

Short-chain fatty acids (SCFAs): molecules produced by microbes during fermentation of carbohydrates and proteins that serve as energy sources and signaling molecules for hosts

Vertical transmission: transmission of microbes between parent and offspring across generations

Oligosaccharide: complex carbohydrate

Horizontal gene transfer: transfer of genetic material between microbial taxa

Prior to weaning, the human gut microbiome exhibits a fairly consistent profile across populations, consisting of low taxonomic diversity that is initially dominated by the bacterial genera *Lactobacillus*, *Bifidobacterium*, *Rothia*, *Enterococcus*, *Streptococcus*, and *Veillonella* (Bäckhed et al. 2015). This profile is maintained at least partially through ecological selection mediated by oligosaccharides present in human breast milk, which are the third most abundant component in milk (after fat and lactose) but cannot be digested by the infant and instead appear to target the gut microbiota and its immunomodulatory functions (Fehr et al. 2020). That mothers invest resources to synthesize compounds targeting the gut microbiota suggests important influences of the gut microbiome on human fitness and evolution, particularly as lactation is energetically costly and can therefore be expected to have been under intense selection pressure in energy-limited environments. Humans appear to synthesize a greater quantity and diversity of milk oligosaccharides than do closely related primates (Hinde & German 2012), with a given mother synthesizing a subset of known human milk oligosaccharides (Smilowitz et al. 2014). Moreover, oligosaccharide composition is heritable, variable over the course of lactation, and responsive to infant health status (Allen-Blevins et al. 2015), hinting at intriguing gene-environment interactions that remain to be elucidated.

With the introduction of supplemental foods and the cessation of breastfeeding, ecological niches within the gut broaden and the microbiome rapidly increases in diversity (Bäckhed et al. 2015), reaching adult-like profiles by the age of 2–3 years (Yatsunenko et al. 2012), although the gut microbiomes of children can remain less complex than those of adults until middle childhood (Roswall et al. 2021). After children wean, population-level differences in the gut microbiota grow more distinct, shaped by local ecology (**Figure 1**). Consistent lifestyle-based differences in gut microbiota composition have been observed across geographically dispersed populations, suggesting convergence in the gut microbial response to shared ecological features. For instance, industrialized lifestyles across continents have been associated with reduced bacterial diversity (Moeller et al. 2014, Smits et al. 2017, Yatsunenko et al. 2012); relative decreases in the bacterial families Prevotellaceae, Spirochaetaceae, and Succinivibrionaceae; and attendant relative increases in the genera *Bacteroides*, *Akkermansia*, and *Bifidobacterium* (Sonnenburg & Sonnenburg 2019a). The impacts of these lifestyle-induced compositional changes on human physiology remain unclear. Several authors have argued that recent changes in the industrialized microbiota may perturb host-microbiota relationships shaped over evolutionary time and therefore that restoring a nonindustrialized-like state may benefit health in industrialized populations (Blaser 2016; Dominguez Bello et al. 2018; Sonnenburg & Sonnenburg 2019a,b). However, the ability of the gut microbiome to adapt rapidly to ecological change raises the possibility that some industrialization-related changes in the gut microbiome could be neutral or even beneficial for the host (Carmody et al. 2021). Although gut microbial taxa undergo selection benefiting their own fitness interests, some capacities benefiting microbial taxa may be indirectly advantageous to the host. For instance, in several Asian human populations, the gut microbiome has acquired porphyranase genes from marine microbes via horizontal gene transfer that permit enhanced digestion of seaweed, a common ingredient in many Asian diets (Hehemann et al. 2010, Pudlo et al. 2022). With gut microbial

plasticity acting as a double-edged sword—in theory, capable of causing biological mismatch while simultaneously enabling rapid adaptation to novel environments—a key research priority is to disentangle the conditions under which restoring aspects of the gut microbiome may be beneficial versus detrimental for health (Carmody et al. 2021).

While individual adults have unique gut microbial signatures that exhibit substantial resilience to long-term perturbation (Lozupone et al. 2012), the structure and function of the gut microbiome are nevertheless dynamic, showing substantial plasticity in response to day-to-day variation in diet (David et al. 2014), xenobiotic exposure (Vich Vila et al. 2020), immune activation (Zheng et al. 2020), and other changes in host physiology (Karl et al. 2018). However, despite substantial variation in gut microbiota composition within and across populations and individuals, there is greater overlap across hosts in microbial gene content than in microbiota composition (Turnbaugh et al. 2009). The extent to which individual- or population-level microbiomes vary in their ability to carry out core functions, such as fermentation or xenobiotic metabolism, remains to be determined. Emerging studies suggest that at least some microbial functions vary with lifestyle; industrialized gut microbiomes are enriched in genes for antimicrobial resistance and degradation of mucins and glycans, whereas nonindustrialized microbiomes are enriched in genes for the degradation of starch and glycogen (Sonnenburg & Sonnenburg 2019a, Wibowo et al. 2021). Nevertheless, there is extensive uncharacterized genomic variation across human gut microbiomes, especially among nonindustrialized populations (Pasolli et al. 2019), and a relative paucity of data on uncultivated microbial genomes (Nayfach et al. 2019). Therefore, inherent knowledge gaps exist in functional comparisons of microbiomes across populations.

Xenobiotic: a nonnutritive substance that is foreign to the body such as a medication or plant toxin

Microbial genome: the genome of a single microbial taxon

Coprolite: fossilized feces

CHANGES IN THE HUMAN MICROBIOME ACROSS EVOLUTION

Industrialized microbiomes show evidence of particularly rapid evolution, including accelerated rates of horizontal gene transfer that likely reflect gut microbial adaptation to novel environmental pressures (Groussin et al. 2021). However, the human gut microbiome has doubtless been shaped by innovations throughout our evolutionary history, such as expansion into new geographies (Suzuki & Ley 2020), cooking (Carmody et al. 2019), agriculture (Poole et al. 2019), and animal domestication (Reese et al. 2021a, Schmidt et al. 2020).

Understanding the evolution of the human gut microbiome requires knowledge of past microbial profiles. However, assessment of ancestral microbiomes is not straightforward. Reconstructing the evolutionary history of gut microbiomes through genomic techniques is complicated by the large number of microbial genomes involved; changes in community composition over daily (David et al. 2014), seasonal (Davenport et al. 2015, Smits et al. 2017), and generational timescales (Sonnenburg et al. 2016); in situ evolution of individual taxa during the lifetime of a single individual aided by short microbial generation times and horizontal gene transfer (Garud et al. 2019); and large differences in nucleotide substitution rates across bacterial genomes that erode the utility of molecular clocks (Duchêne et al. 2016). Therefore, our knowledge of past human microbiomes has largely been assembled by other techniques.

Analysis of ancient feces (coprolites) provides the most direct approach for characterizing past microbiomes. However, the availability of coprolites is limited, and successful characterization of the original gut microbial community is complicated because excreted communities are subject to rapid degradation and contamination by environmental microbes. Even under the most favorable circumstances—e.g., deposition in extremely dry, salty, or frozen environments with limited taphonomic disturbance—assessing community-level composition from coprolites has proven inconsistent (Warinner et al. 2015). Available studies of coprolites dated to 1,000–2,000 years concur that these ancestral human microbiomes were more similar to those of contemporary nonindustrialized populations than to those of industrialized populations (Tito et al. 2012,

Wibowo et al. 2021). In a recent study involving large-scale de novo assembly of microbial genomes, eight coprolites from Utah and Mexico harbored numerous taxa that have not been detected in modern populations (Wibowo et al. 2021). These ancient microbiomes exhibited lower abundances of antibiotic-resistance genes and mucin-degrading genes compared with contemporary industrialized gut microbiomes. Neanderthal fecal deposits dating to ~50 kya have also been analyzed recently; detection of several contemporary gut commensal genera (e.g., *Alistipes*, *Bacteroides*, *Bifidobacterium*, *Desulfovibrio*, *Faecalibacterium*, *Prevotella*, *Roseburia*, *Ruminococcus*) suggests that the association of these taxa with humans may have predated the split between the human and Neanderthal lineages (Rampelli et al. 2021).

Comparative approaches can also help establish broad patterns in human gut microbiome evolution. Compared with our closest living relatives in *Pan* and *Gorilla*, the human microbiome across both industrialized and nonindustrialized populations shows evidence of generalized reduced taxonomic diversity, enrichment in several genera (*Alistipes*, *Bacteroides*, *Bifidobacterium*, *Clostridium*, *Faecalibacterium*, *Paraprevotella*, *Roseburia*, *Subdoligranulum*, *Streptococcus*), and depletion in others (*Dialister*, *Fibrobacter*, *Methanobrevibacter*, *Olsenella*, *Slackia*, *Sporobacter*, *Syntrophococcus*) (Moeller et al. 2014). However, the human gut microbiota is more similar to that of cercopithecines, such as baboons, than to that of other African apes (Amato et al. 2019b). The microbial differences observed between humans and nonhuman apes may reflect our divergent evolutionary paths from our last common ancestor. Analysis of strain-level bacterial diversity suggests that members of the Bacteroidaceae and Bifidobacteriaceae families have been closely associated with their respective hosts since the divergence of the host lineages (Moeller et al. 2016). However, data from across the primate phylogeny suggest that as little as 3% of microbial taxa are codiversifying with their hosts, with many taxa being more ancient than their hosts (Amato et al. 2019c). Moreover, humans across cultures appear to have experienced accelerated extinctions of microbial taxa bearing evidence of codiversification within the primate clade, with losses of codiversified taxa exceeding losses of non-codiversified taxa (Sanders et al. 2023). Jointly, these signatures point to unique aspects of host physiology or ecology encouraging colonization by specific microbial taxa above and beyond background signatures of codiversification.

Overall, the evidence available from coprolites and comparative studies suggests that human microbiomes have lost diversity over evolutionary time but have retained long-standing relationships with key taxa that are hypothesized to play critical roles in human biology. However, evidence that human gut microbiota can more closely resemble those of cercopithecines than those of African apes, coupled with evidence that humans have lost codiversified microbial taxa at a faster rate than non-codiversified taxa, underscores that the influence of ecology generally outweighs that of phylogeny in shaping the human gut microbiome.

PROCESSES GOVERNING EVOLUTIONARY CHANGES IN THE GUT MICROBIOME

The processes determining compositional change and host-microbial codiversification during human evolution remain unknown, but they have been interpreted to reflect ecological changes, such as increased dependence on animal foods at the expense of dietary fiber (Moeller et al. 2014; Smits et al. 2017; Sonnenburg & Sonnenburg 2019a,b), as many of these patterns are most pronounced in industrialized populations. Nevertheless, concordance between ecological niches and changes in the microbiome provides little information regarding causality. While changes in the human ecological niche are widely assumed to have driven changes in the microbiota, a key unanswered question is the extent to which gut microbiota may have enabled exploitation of new ecological niches by humans.

The human gut microbiome possesses a metabolic capacity that vastly exceeds that of the human genome (Koppel et al. 2017), and day-to-day plasticity in response to changes in the luminal environment makes the gut microbiome a highly adaptable ecosystem within the comparatively static human body. The role of gut microbial plasticity in human evolution remains unclear but can be expected to have increased the capacity of humans to accommodate some ecological challenges (Amato et al. 2019a, Carmody et al. 2021, Kolodny & Schulenburg 2020). For instance, evidence that the human gut microbiome adapts on daily timescales to diets rich in animal foods versus plant foods, exhibiting altered patterns of gene expression that overlap with those documented in carnivores versus herbivores, suggests that the gut microbiome may help humans accommodate short-term changes in foraging success (David et al. 2014). Similarly, evidence that changes in the gut microbiome serve to augment host energy balance when diets are low in digestibility and high in xenobiotic load suggests that the gut microbiome may serve as a dynamic buffer against low dietary quality (Carmody et al. 2019). Such capacities could have meaningful effects on fitness, especially in populations experiencing substantial daily and seasonal volatility in food supply.

The gut microbiota consists of microbial taxa with divergent fitness interests, and these fitness interests may only rarely align with those of the host (Foster et al. 2017). Moreover, the host will not necessarily exploit niches opened by the gut microbiome, nor can we necessarily expect to see genomic evidence of host adaptation to such niches, even when they increase fitness (Kolodny & Schulenburg 2020, Suzuki & Ley 2020). Identifying instances in which gut microbial capacities may have enabled niche expansion in humans is therefore difficult.

The most promising evidence of microbiome-directed niche expansion in humans may ultimately be found in cases where humans cannot successfully exploit a current niche, or could not have easily begun to exploit a niche, without contributions from the gut microbiome. For instance, the selective pressures surrounding the early stages of human milk consumption in adulthood, prior to genomic adaptations for lactase persistence, remain unclear (Ségurel & Bon 2017). Ancient populations may have been consuming primarily fermented milk products, which are depleted in lactose (Ségurel et al. 2020). However, another possibility is that baseline variation in the gut microbiome may have allowed some individuals to consume this novel food resource with fewer side effects and/or to achieve higher energy returns than others (Goodrich et al. 2017, Ségurel & Bon 2017), thus increasing the probability that they would consume it. Increased exposure may have then provided opportunities for selection to act on the human genome to improve direct host capacity for lactose digestion, which would be advantageous because SCFAs derived from microbial fermentation of lactose deliver to the host approximately half the energy gained from digesting lactose directly (Carmody & Wrangham 2009, Cummings & Macfarlane 1997). To this end, numerous studies have reported links between alleles conferring lactase persistence and reduced abundance of *Bifidobacterium* spp., a genus possessing broad capacities for lactose fermentation (Blekhman et al. 2015, Bonder et al. 2016, Kato et al. 2018). Increases in *Bifidobacterium* and other lactose-fermenting genera such as *Faecalibacterium* and *Lactobacillus* have been correlated with decreased symptoms of lactose ingestion in lactase nonpersistent individuals (Azcarate-Peril et al. 2017). Moreover, the degree of microbial protection against symptoms increases with exposure to lactose (Forsgård 2019), creating a feedback loop in which functions provided by the gut microbiome encourage niche exploitation and vice versa. Such processes suggest that the gut microbiota may have facilitated early and frequent exposure of humans to lactose, setting the stage for later genomic adaptation in some, but not all, dairying populations (Suzuki & Ley 2020). Once a function is encoded in the human genome, the gut microbiome may also contribute to relaxing selection pressure by providing functionality in the absence of selected alleles, thereby reducing fitness differentials across individuals and maintaining polymorphisms.

Horizontal transmission: transmission of microbes between an individual and the environment, nonparent conspecifics, or other organisms

The gut microbiome can likewise be expected to have modified the adaptive landscape for humans in many other scenarios (Suzuki & Ley 2020). These include instances where (*a*) the gut microbiome is capable of synthesizing nutrients essential for humans, such as vitamin B (Uebanso et al. 2020); (*b*) the gut microbiome exerts control over a host physiological function relevant to dietary change, such as bile acid metabolism (Chadaideh & Carmody 2021), or to adaptation to new environments, such as cold-induced thermogenesis (Chevalier et al. 2015, Worthmann et al. 2017); (*c*) humans and microbes both benefit from a common objective, such as the exclusion of virulent pathogens like cholera (Hsiao et al. 2014); and/or (*d*) humans and microbes compete directly for resources, as in the case of evolutionary trends toward high dietary digestibility, which likely favored adaptations restricting microbiota encroachment into the small intestine (Walter & Ley 2011). Although it will be challenging to detect specific influences of the gut microbiome on human genomic evolution, microbial involvement in essential physiological processes and the phenotypic expression of human genes bearing signals of selection are attractive candidates for targeted study.

LEVERAGING NONHUMAN PRIMATES TO ASSESS MICROBIAL INTERACTIONS WITH HOST ECOLOGY AND EVOLUTION

Data from modern human populations reflect diverse and often uncharacterized cultural influences on lifestyles, health, reproduction, and survival, and data from coprolites often lack key contextual data that are necessary to interrogate complex host-microbiome-environment interactions. In contrast, wild nonhuman primates are well-studied; detailed ecological data are available for multiple species ranging from the individual to the population level. In addition to being closely genetically related to humans, nonhuman primates live in dynamic environments that can provide insight into the selective forces shaping ecology and evolution. Finally, the wide diversity of ecologies and evolutionary trajectories represented within the primate phylogeny can be used to test hypotheses concerning the importance of different factors in host-microbe relationships.

Strong evidence indicates that host ecology and evolution influence nonhuman primate gut microbiomes both within and across primate species. As observed in humans, studies within single nonhuman primate species demonstrate that interindividual variation in the gut microbiome is shaped by various host factors, including age/sex (Amato et al. 2014, Reese et al. 2021b), diet (Amato et al. 2015, Hicks et al. 2018), social interactions (Perofsky et al. 2017, Tung et al. 2015), and genetics (Grieneisen et al. 2021). However, in many cases the nonhuman primate literature is better positioned to quantify the effects of these factors, given lesser potential confounds and greater data richness. For example, detailed social networks constructed from behavioral data can describe how often and in what ways nonhuman primates interact, providing a more quantitative basis for tracking horizontal transmission than is often possible in human studies (Perofsky et al. 2017). Similarly, by integrating decades of longitudinal data describing microbiome taxonomic composition, host genetics, and diet/seasonality, a recent study of baboons was able to demonstrate and quantify heritability of microbial traits to an extent that is not currently feasible in human studies (Grieneisen et al. 2021).

Nonhuman primates are also a useful system to explore the effects of the gut microbiota on host ecology and evolution. An early study focused on understanding how the gut microbiota might help buffer black howler monkeys against temporal changes in food availability, allowing them to persist in seasonal environments. Data demonstrated that during periods when black howler monkeys consumed less easily metabolizable energy in their diet, gut microbiome composition shifted and fecal concentrations of SCFAs, utilizable by hosts for energy, increased (Amato et al. 2015). Notably, increased gut microbial contributions to host energy status under short-term conditions

of reduced dietary digestibility have also been observed in mice (Carmody et al. 2019), raising the possibility that this is a broader biological phenomenon. Studies of other primate species also demonstrate seasonal shifts in gut microbiome composition (Baniel et al. 2021, Cui et al. 2022, Gomez et al. 2016, Hicks et al. 2018, Orkin et al. 2019, Springer et al. 2017). However, many lack detailed dietary data or information about SCFA production, making the causes and effects of these seasonal patterns difficult to disentangle. Evidence also suggests constraints on the capacity of the gut microbiome to buffer hosts against environmental change. In black howler monkey populations inhabiting fragmented forests, microbial diversity and the relative abundances of SCFA-producing microbes are reduced while the relative abundances of potential pathogens are increased (Amato et al. 2013). Therefore, the gut microbiota is not buffering monkeys in these habitats, and it may be actively contributing to health risks. This study, and another in sifakas (McManus et al. 2021), suggests that these microbial dynamics are related to diet. In gorillas, stress from exposure to humans has also been shown to negatively alter the microbiome (Gomez et al. 2015). Additional research quantifying the gut microbial consequences of anthropogenic habitat change, and the concordances of these signatures with those emerging in industrialized and developing human populations, will provide further insight into the potential mechanisms underlying these microbiome differences and downstream health impacts for primates and humans alike.

Comparative data across primate species allow us to formulate and test generalizable rules about host-microbe interactions across the phylogeny. Current data gaps notwithstanding, it is clear that the relative importance of different host and environmental factors in shaping the gut microbiome varies by species. For example, the baboon gut microbiome appears to be most strongly shaped by environmental microbial exposure and social interactions (Grieneisen et al. 2019, Tung et al. 2015), while the black howler monkey gut microbiome appears to be most strongly shaped by diet (Amato et al. 2015). Additionally, the black howler monkey gut microbiome shifts in a predictable manner across seasons, while the baboon microbiome varies to a similar degree across days, months, and years (Amato et al. 2015, Grieneisen et al. 2019, Tung et al. 2015). Despite signals of differential interactions with ecology, comparative nonhuman primate studies indicate that host species-specific microbiomes are conserved across space and time (**Figure 2**). Regardless of how much an individual's diet changes over time or in what location a species is sampled, cross-species differences in gut microbiome composition and function are maintained in wild populations (Amato et al. 2019c). Even instances of microbial convergence between sympatric species are not strong enough to dampen this signal (Moeller et al. 2013). Only captivity, which is known to substantially alter the gut microbiota of many host species, particularly those with more specialized diets, has been reported to interrupt this pattern in some instances (Clayton et al. 2016, Frankel et al. 2019, Reese et al. 2021a). However, even in these cases, microbial differences between host species remain evident. Evolved traits related to immune function and digestive physiology are likely to be important drivers of these cross-host species patterns (Amato et al. 2019c, Mallott & Amato 2021). As a result, the primate gut microbiota is both shaped and constrained by host evolutionary history, and conserved host-microbe interactions also have the potential to shape and constrain host evolutionary systems.

GENERALIZABILITY OF NONHUMAN PRIMATE HOST-MICROBIOME PATTERNS TO HUMANS

Findings from nonhuman primates are likely to enrich our understanding of human gut microbiome dynamics, given broad similarities in the physiological traits that interact with the microbiome and a variety of shared microbial taxa. Nevertheless, early research suggests key differences in the human gut microbiome that could indicate a unique relationship between the gut microbiome and host ecology and evolution.

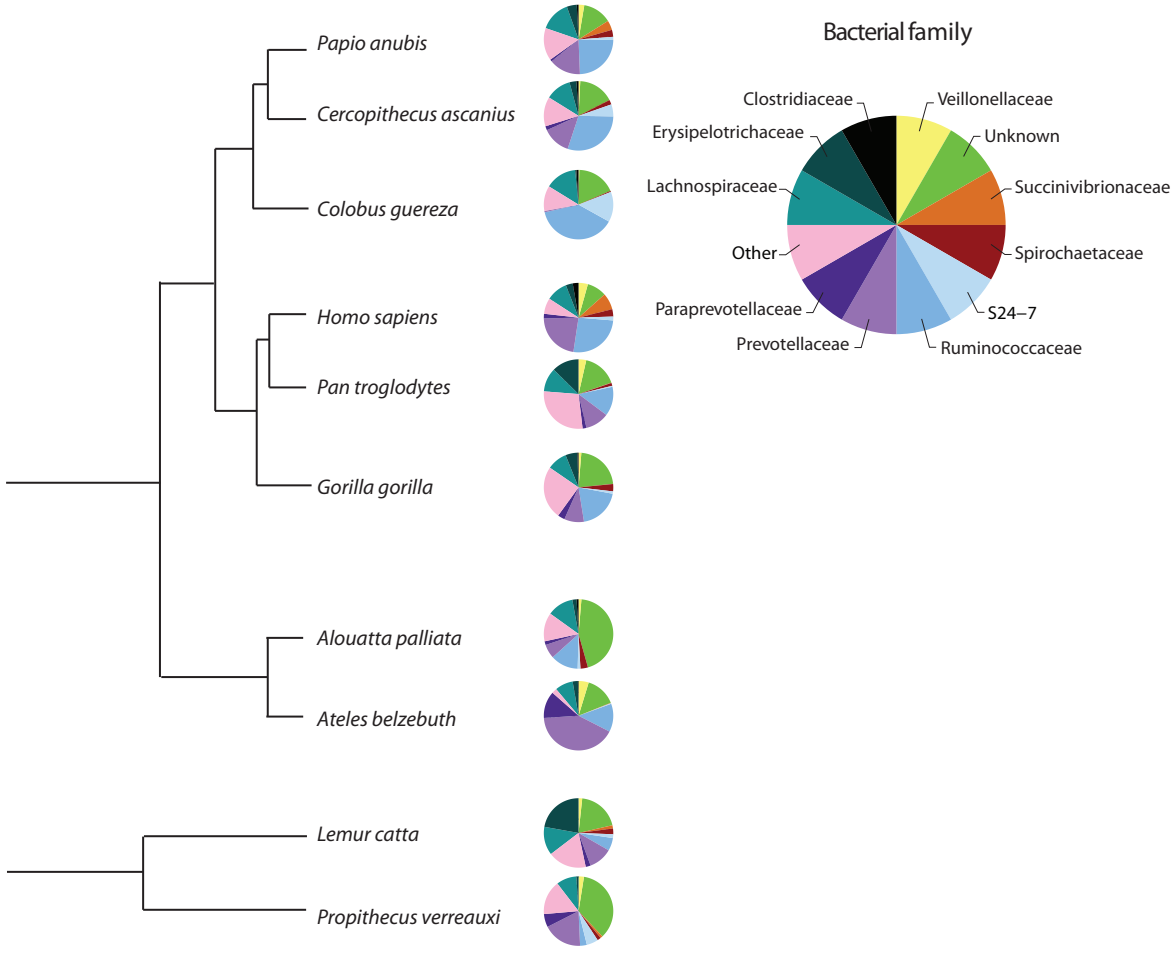

Figure 2

Family-level taxonomic composition of the gut microbiota of representative members of the order Primates. The human gut microbiota is equally dominated by the families Prevotellaceae and Ruminococcaceae, a pattern that is most closely mirrored by cercopithecines: *Papio anubis* and *Cercopithecus ascanius*. Data originate from Amato et al. (2019b), and human data derive exclusively from nonindustrialized populations. The phylogenetic tree represents primate phylogenetic relationships to each other.

First, the human gut microbiome appears to have changed more rapidly over time than those of other apes (Moeller et al. 2014) and bears evidence of losing codiversified microbial taxa at an accelerated rate (Sanders et al. 2023). Accordingly, the human gut microbiome breaks the host phylogeny-paralleling pattern observed in other primates, with the human gut microbiome demonstrating more similarities to those of cercopithecine primates than to those of more closely related apes (Amato et al. 2019b, Gomez et al. 2019). This pattern is hypothesized to be a product of convergence in human and cercopithecine ecological niches, particularly diet; the omnivorous diet of cercopithecines occupying more open, woodland habitats is more similar to that of humans versus the highly frugivorous diets of other apes occupying rainforest habitats. The microbiomes of humans and nonhuman apes do exhibit similarities, though, raising the possibility that the human microbiome represents a sort of hybrid between cercopithecine and ape microbiomes due to joint ecological and evolutionary causes. If so, the resulting microbial services could have facilitated

survival as humans transitioned to a more cercopithecine-like habitat. What those services are and which microbial traits they are associated with remain to be identified. However, taxa including *Helicobacter pylori*, *Bacteroides fragilis*, *Faecalibacterium prausnitzii*, and *Streptococcus salivarius* are generally enriched in humans compared with both apes and cercopithecines (Amato et al. 2019b).

Second, the human gut microbiome is distinct from that of other primates in that it exhibits increased interindividual variation, particularly with regard to functional potential (Amato et al. 2019b). Humans are the most widespread primate on the planet and have had to confront an astounding diversity of diets and infectious disease landscapes during migrations to new habitats and/or withstand climate shifts over time in the same habitat. Because host diet and immunity are so tightly linked to the gut microbiome in a bidirectional manner, these important dynamics in human evolution seem likely to be associated with the unique dynamics observed in the human microbiome. Human food processing techniques including fermentation (Amato et al. 2021) and cooking (Carmody et al. 2019) and the domestication of plants and animals intended for consumption (Jha et al. 2018) are also likely to contribute, particularly as cultural influences led to divergence in local human ecologies across populations.

Other unique aspects of human physiology and ecology suggest that we might expect differences in human and nonhuman primate host-microbe relationships. Human life-history traits, including the lengths of the juvenile period, interbirth intervals, and life span, all differ from those of other primates and have been linked to a suite of social and metabolic traits that are believed to facilitate them (Aiello & Wells 2002, Kaplan et al. 2000, Kramer 2010, Leonard & Robertson 1992, Wrangham & Carmody 2010). For example, allocare and the availability of suitable weaning foods are believed to allow human mothers to wean their offspring earlier than would otherwise be possible, thus shortening interbirth intervals. Social interactions directly and indirectly influence the gut microbiota (Sarkar et al. 2020), as does the composition of breast milk (Boudry et al. 2021), weaning schedule (Bäckhed et al. 2015), dietary composition (Boudry et al. 2021, David et al. 2014), and habitual cooking (Carmody et al. 2019, Smith et al. 2015). Differences in these factors in humans versus nonhuman primates may contribute to the recent observation that gut microbial diversity exhibits opposite patterns in humans and chimpanzees over the first two years of life. Human infant microbiota start out with few unique taxa then rise rapidly in diversity, while chimpanzee infants begin life with very high gut microbial diversity that drops rapidly with age (Reese et al. 2021b). Similarly, humans have higher fasting blood glucose and increased adiposity compared with most other primates (Cai et al. 2004, Heldstab et al. 2016, Kern et al. 2003, Tigno et al. 2004, Tirosh et al. 2005, Wagner et al. 2006). The microbiome plays a causal role in programming glucose homeostasis and fat storage in the context of both health and disease (Blekhman et al. 2014, Carmody & Bisanz 2023, Kimura et al. 2020, Lynch & Pedersen 2016, Utzschneider et al. 2016), suggesting that metabolic relationships between humans and our microbiota may differ from those of other primates. Exploring these relationships is likely to advance the study of human evolution in novel ways, by casting a new lens on interspecific, population-based, and individual phenotypic variation, and through broader appreciation that some signals of human evolution may be encoded in the microbial metagenome.

CONCLUSIONS

Integrating knowledge of the human gut microbiome across time and space as well as knowledge of host-microbiome-environment interactions in nonhuman primates can provide us with a strong framework for exploring tripartite impacts between the microbiome, human ecology, and human evolution. As we continue to cut across disciplines, combining methods and perspectives, we expect the pace of discovery to accelerate and for the microbiome to increasingly be viewed as an intrinsic part of human biology and an essential force that has shaped our evolutionary journey.

Although there is a continued need for descriptive research that measures gut microbial variation in response to a range of host and environmental factors across human and nonhuman primate populations, there is also a strong need for studies that more quantitatively test generalizable rules of host-microbe interactions. Therefore, studies must move beyond qualitative temporal and spatial comparisons and include quantitative assessments of host and environmental traits. We must also incorporate experimental tools and techniques into our work that allow for more rigorous examination of microbial functions and their impacts on host health. In addition to documenting taxonomic or genomic shifts in the microbiome, we need better insight into microbial function via data on transcription and metabolite production. The value of basic host physiological data is also becoming increasingly clear. Gut anatomy, enzyme activity, and pH are likely to shape the gut microbiome as are the immune system, social behavior, and other aspects of host biology. However, in many cases, systematically collected data describing these factors are not available. Placing a renewed emphasis on gathering basic health and natural history data will help accelerate the field in ways that may not be currently appreciated. Finally, approaches that establish microbiome-to-phenotype causation, such as gnotobiotic transplant experiments, will be a critical complement to observational studies. In vivo experiments that test microbial responses to aspects of host diet or different host immune environments as well as in vivo, ex vivo, or in vitro experiments that discriminate the independent effects of phylogeny, physiology, and current ecology on primate gut microbiota and the downstream consequences for host biology are expected to be especially informative.

Emerging insights into host-microbiome interactions can make important contributions to our understanding of human biological variation, human evolution, and nonhuman primate ecology, evolution, and conservation. Determining the extent to which host-microbiome interactions are more or less biologically consequential than other forms of host-environment interactions, and the phenotypic consequences of perturbing these interactions through ecological change, will be critical for moving these fields of anthropology forward. The pervasive influence of the gut microbiome on human physiology, the wide range of potential microbial interactions with culture and lifestyle, and the implications for many of the central frameworks of human ecology and evolution make it an especially exciting time to revisit anthropology through a microbial lens.

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