MICROBIOTA

Seasonal cycling in the gut microbiome of the Hadza hunter-gatherers of Tanzania

Samuel A. Smits,[1]* Jeff Leach,[2,3]* Erica D. Sonnenburg,[1] Carlos G. Gonzalez,[4] Joshua S. Lichtman,[4] Gregor Reid,[5] Rob Knight,[6] Alphaxard Manjurano,[7] John Changalucha,[7] Joshua E. Elias,[4] Maria Gloria Dominguez-Bello,[8] Justin L. Sonnenburg[1]†

Although humans have cospeciated with their gut-resident microbes, it is difficult to infer features of our ancestral microbiome. Here, we examine the microbiome profile of 350 stool samples collected longitudinally for more than a year from the Hadza hunter-gatherers of Tanzania. The data reveal annual cyclic reconfiguration of the microbiome, in which some taxa become undetectable only to reappear in a subsequent season. Comparison of the Hadza data set with data collected from 18 populations in 16 countries with varying lifestyles reveals that gut community membership corresponds to modernization: Notably, the taxa within the Hadza that are the most seasonally volatile similarly differentiate industrialized and traditional populations. These data indicate that some dynamic lineages of microbes have decreased in prevalence and abundance in modernized populations.

The gut microbiota (or microbiome) is an integral part of host biology, influencing immune function and development, metabolism, and the central nervous system (*1*–*3*). This complex community of microbes must be reassembled each generation since before birth, infants lack a gut microbiota. Microbial lineages appear to be vertically transmitted (*4*, *5*) and have been associated with the human lineage for >15 million years (*6*). Microbiota composition is sensitive to diverse perturbations, including dietary change and the invasion of enteric pathogens (*7*, *8*). The resilience of a microbiota community is quite individual: Some people experience a return to their starting state after perturbation (*9*, *10*), whereas in others, new stable states may appear (*11*, *12*), which can become pathological. However, most information about human gut microbiota dynamics is collected in the context of responses to antibiotic treatments and described in humans living in an urban setting, which have decreased diversity and different microbiota membership as compared to the gut communities of populations living traditional lifestyles (*13*–*18*). Indeed, a previous report of stool microbiomes collected from 27 Hadza hunter-gatherer individuals at a single time point revealed a high degree of bacterial diversity (*19*). Here, we have performed an in-depth, longitudinal analysis of the Hadza hunter-gatherer microbiome to provide insight into the dynamics of a diverse gut microbiota in a nonindustrial, nonurban setting.

The Hadza, a community residing near Lake Eyasi in the central Rift Valley of Tanzania, are among the last remaining populations in Africa that live a hunter-gatherer lifestyle (*20*). Today there are fewer than 200 Hadza that adhere to this traditional way of life. They live in camps with approximately 5 to 30 people per camp, although camp numbers vary depending on the season and available resources (*21*). As a result of encroachment on limited land and rapid transculturation, including increasing exposure to medicines and processed foods, the Hadza way of life is disappearing (*20*). We collected 350 fecal samples with informed consent from two culturally and geographically similar camps located within 7 km of each other during a 12-month period spanning five subseasons (fig. S1), representing 188 recorded unique individuals (table S1). To overcome potential biases that repeated sampling might introduce, we limited all analyses in this study to a single sample from each individual, unless otherwise noted. On collection, the samples were immediately stored in liquid nitrogen and maintained frozen during all transport and storage until processing for analysis.

The Hadza's activities are largely based around food acquisition. They are affected by the local environment and are subject to two distinct seasons: wet (November to April) and dry (May to October). For example, berry foraging and honey consumption are more frequent during the wet season, whereas hunting is most successful during the dry. Consumption of fiber-rich tubers and baobab occurs year-round (*19*, *20*). We applied principal coordinates analyses (PCoA) to UniFrac distances of 16*S* ribosomal RNA (rRNA) amplicon profiles generated from samples collected from two dry and one wet season (Fig. 1A). Differences in microbiome composition between two seasons have been observed in the agricultural Hutterites of the USA (*22*). The microbiomes of individual Hadza, when plotted by season, revealed cyclical features: Microbiotas from the dry seasons in sequential years were indistinguishable from one another yet were distinguishable from the intervening wet-season microbiota ($P < 3 \times 10^{-15}$ and $P < 3 \times 10^{-16}$, Wilcoxon; Fig. 1A).

We compared our data set with microbiome profiles previously reported for the Hadza (*19*) and U.S. residents (Human Microbiome Project; HMP) (*23*). This analysis revealed commonalities in the taxonomic representation of bacteria within the two Hadza data sets, which, independent of season, segregated from the microbiome of U.S. residents (Fig. 1B, top panel). Notably, the previously reported single-season collection from the Hadza fit the cyclic pattern of microbiome reconfiguration (Fig. 1B, bottom panel). Both higher phylogenetic diversity and greater numbers of unique operational taxonomic units (OTUs) were observed in the dry seasons as compared with the wet season (fig. S2A).

To understand what might be driving the cyclical pattern, we examined the OTUs that are maintained in the Hadza across the phylogenetic shifts through the seasons. Firmicutes composition remained relatively stable throughout the sampling period, whereas Bacteroidetes OTUs, primarily those of the Prevotellaceae, declined significantly in the wet season (fig. S2B). Examining commonly shared OTUs, present in at least 10% of the individuals, season by season revealed a pronounced constriction of Bacteroidetes in the early-wet season (62.8% decrease in shared OTUs for late-dry–2013 to early-wet–2014, representing 4.4 standard deviations (SDs) from the means of all other seasons; Fig. 1C). By contrast, the shared number of Firmicutes, remained relatively stable across the seasons (0.21 SD; fig. S2C).

Tracking individual OTUs within different phyla revealed distinct temporal dynamics within the Bacteroidetes and Firmicutes. Many of the Bacteoidetes OTUs display seasonal volatility, with 70.2% disappearing between 2013–late-dry and 2014–early-wet; 78.2% of those that disappeared, reappeared at later time points (Fig. 1D, left panel). A smaller proportion of the Firmicutes OTUs showed this seasonal cyclic pattern. The greatest number of Firmicutes OTUs disappear between 2014–late-wet and 2014–early-dry (62%); 76% of those are detected at other time points (Fig. 1D, right panel). A supervised learning approach that specifically attempts to

[1]Department of Microbiology and Immunology, Stanford University School of Medicine, Stanford, CA 94305, USA. [2]Human Food Project, 53600 Highway 118, Terlingua, TX 79852, USA. [3]The Department of Twin Research and Genetic Epidemiology, King's College London, St. Thomas' Hospital, Lambeth Palace Road, London SE1 7EH, UK. [4]Department of Chemical and Systems Biology, Stanford School of Medicine, Stanford University, Stanford, CA 94025, USA. [5]Lawson Health Research Institute and Western University, London, Ontario N6A 4V2, Canada. [6]Departments of Pediatrics and Computer Science and Engineering and Center for Microbiome Innovation, University of California, San Diego, CA 92093, USA. [7]National Institute for Medical Research, Mwanza 11101, Tanzania. [8]School of Medicine and Department of Anthropology, New York University, New York, NY, USA.
*These authors contributed equally to this work. †Corresponding author. Email: jsonnenburg@stanford.edu

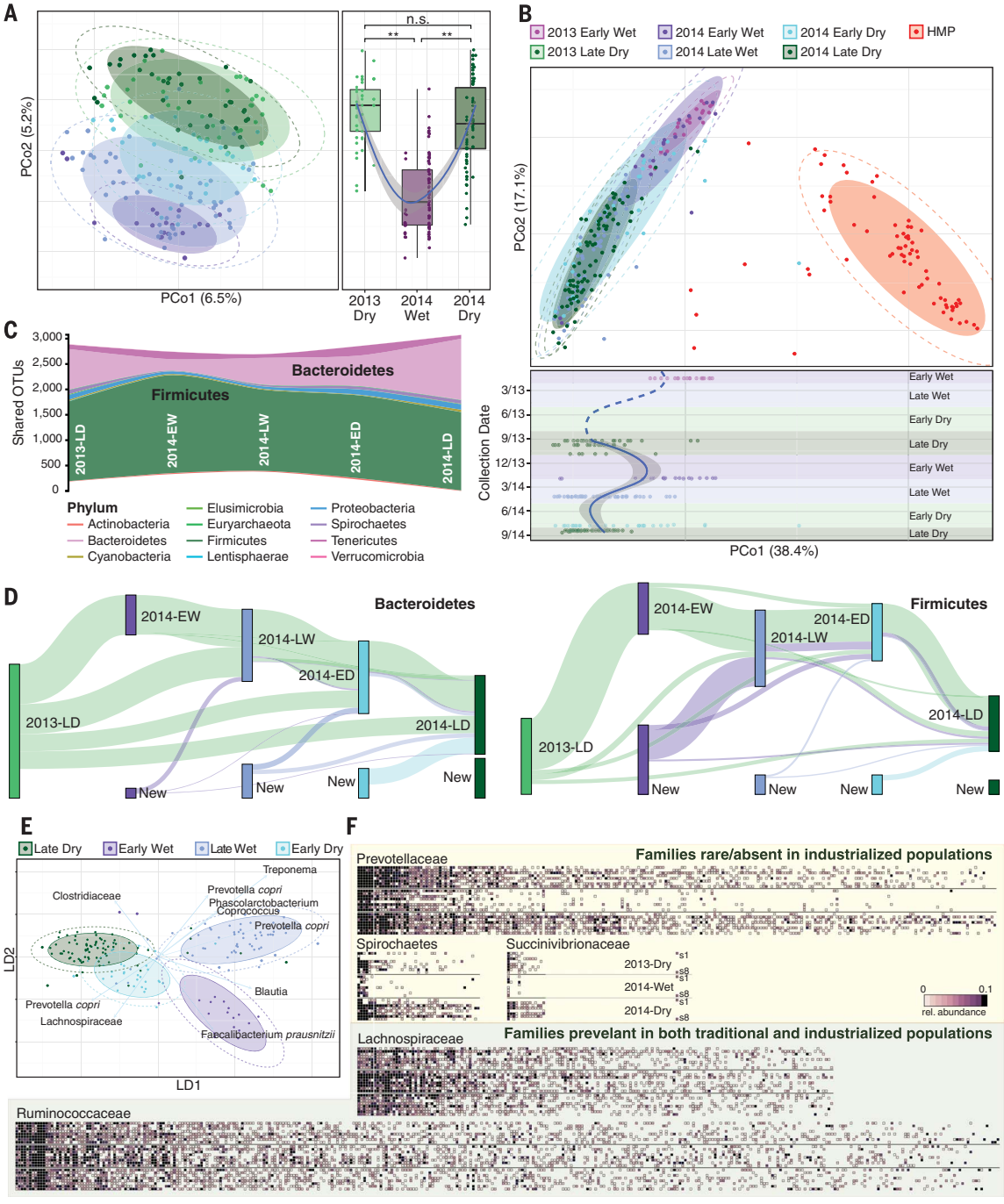

Fig. 1. Hadza gut microbial community compositions are cyclic and can be differentiated by season. (**A**) Individual Hadza gut microbiota compositions in 2013–late-dry (n = 41, light green), 2014–early-wet (n = 19, purple), 2014–late-wet (n = 58, light purple), 2014–early-dry (n = 30, light blue), and 2014–late-dry (n = 40, dark green) subseasons plotted on an unweighted UniFrac PCoA plot (left panel). Samples collected in the dry season are distinct from wet-season samples ($P < 3 \times 10^{-15}$ and $P < 3^{-16}$, Wilcoxon), whereas dry-season samples are indistinct (P = 0.15, Wilcoxon) (right panel). (**B**) Top panel: Individual Hadza gut microbiota compositions from (A) (n = 188), samples collected in 2013 Early Wet in a previous Hadza study (*19*) (n = 20, violet) and the Human Microbiome Project (HMP) (n = 71, red) are shown on a PCoA plot according to their Bray-Curtis dissimilarity at the family taxonomic level. Bottom panel: The Hadza samples across both studies representing 1.75 years are plotted according to their collection date on the y axis, and their position on the x axis is plotted according to their first principal coordinate in the Bray-Curtis PCoA (top panel). The subseasons are labeled and indicated by shading; Loess regression was applied to these points using the collection date and PCo1 coordinates, and the curve was plotted in blue with a 95% pointwise confidence interval band in gray on the plot using the data within this study. The dashed blue line is a continuation of the regression curve, yet is an implied regression curve assuming the appropriate inflection points are captured with data from our study. (**C**) The number of unique OTUs that are present and shared in at least 10% of the population at indicated seasons (LD: late-dry; ED: early-dry; LW: late-wet; EW: early-wet) are aggregated and colored by phylum on a streamgraph. (**D**) OTUs that are shared by at least 10% of the population within each season are tracked using Sankey plots in both the Bacteroidetes and Firmicutes. The heights of the rectangles indicate the relative number of OTUs, and each subseason has a distinct color. The lines represent the transfer of OTUs between seasons and are colored by the first season of appearance. (**E**) Linear discriminant analysis, a supervised learning approach that utilizes a linear combination of features to maximize the separation of classes, successfully separates the subseasons, except for the dry seasons. The length and direction of the arrows indicate the normalized scalings for each of the features (OTUs). (**F**) Heatmaps represent microbiotas from all individuals (n = 8) that were sampled across the wet and both dry seasons. Along the y axis of each heatmap, individuals are ordered similarly across all three seasons. The top eight rows correspond to the individuals' microbiotas in 2013-dry; middle, 2014-wet; bottom, 2014-Dry. Along the x axis are unique OTUs that are found in at least 0.1% of the OTUs across the eight individuals and are sorted (left to right) by their prevalence across all seasons and are shaded according to the relative abundance of OTUs. The shaded ellipses in all plots represent the 80% confidence interval, the dotted ellipse borders represent the 95% confidence interval. All boxplot distributions are tested using the nonparametric two-sided Wilcoxon rank sum test with Holm correction for multiple hypothesis testing; center values indicate the median and error bars the standard deviation (SD); *P < 0.05, **P < 0.01; ns, not significant.

distinguish groups by integrating a linear combination of OTUs was unable to differentiate the same season (dry) in sequential years, supporting the cyclic nature of the reconfiguration (Fig. 1E, fig. S3A, and table S2).

We extended our analysis to determine if other taxa were seasonally volatile or stable. Examining OTUs in the eight Hadza individuals that were sampled across three seasons (fig. S3B) revealed that the Succinivibrionaceae, Paraprevotellaceae, Spirochaetaceae, and Prevotellaceae families were among the most variable across seasons (Fig. 1F and fig. S3C).

Systematic seasonal differences in the Hadza microbiota led us to hypothesize that seasonal dietary changes might lead to related changes in the functional capacity of the microbial community. Previous reports were limited to a single season (*19*, *24*); we therefore selected 35 samples across the seasons (fig. S4A) and performed both shotgun metagenomic sequencing and untargeted metabolomics to gain insight into community functionality.

Comparison of carbohydrate active enzymes (CAZymes) (*25*) encoded in Hadza gut metagenomes to those of healthy American subjects identified a more diverse repertoire for utilizing carbohydrates in the Hadza (Fig. 2, A and B). When comparing the Hadza microbiome across time points, we found no significant differences between the dry-season microbiotas, whereas the wet-season microbiotas possess a significantly less diverse CAZyome compared to the dry-season microbiotas ($P < 0.05$, Wilcoxon). The Hadza microbiotas show greater functional capacity for utilization of plant carbohydrates than the microbiotas of Americans (Fig. 2D; $P < 2 \times 10^{-16}$, Wilcoxon). Our metagenomic data suggest that the microbiotas of healthy Americans have a greater mucin-utilization capacity (indicating less plant material in the diet) than those of the Hadza (Fig. 2, C and D; $P < 2 \times 10^{-16}$, Wilcoxon).

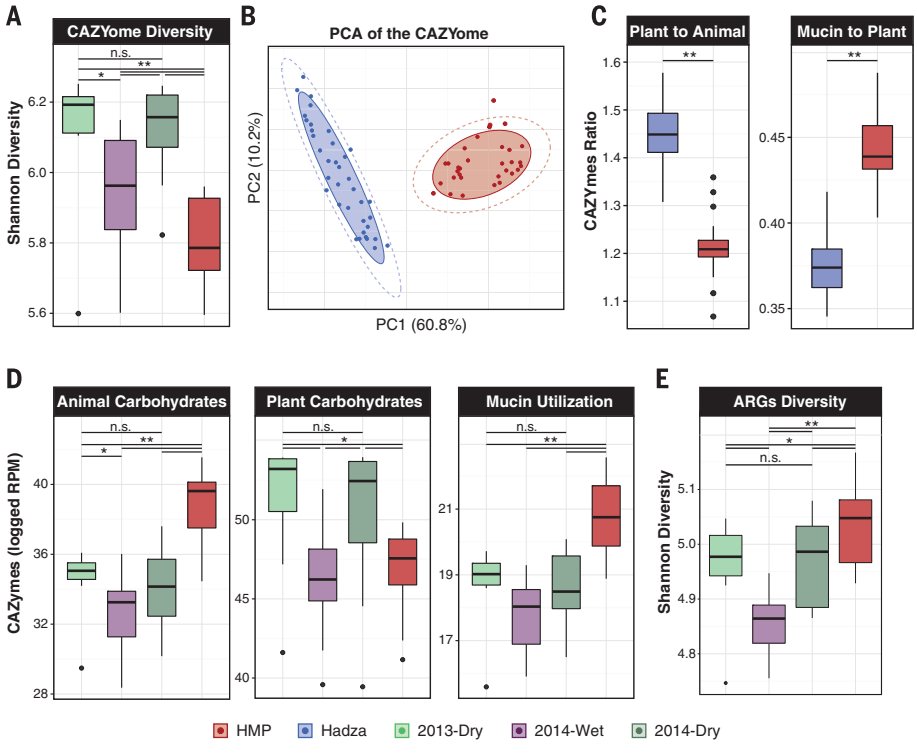

Fig. 2. Hadza gut microbiome functional capacities are cyclic and differentiable by season. (**A**) Shannon diversity metric applied to CAZyome representation in the metagenomic data sets of Hadza by season and for a healthy American cohort (Human Microbiome Project; HMP). (**B**) Principal component analysis (PCA), an unsupervised learning approach that uses a linear combination of features to maximize the variance of the data in a reduced multivariate space, applied to CAZyomes of Hadza and Americans (HMP). The shaded ellipses represent the 80% confidence interval, the dotted ellipse borders represent the 95% confidence interval. (**C**) The ratio of CAZymes represented within the metagenomes related to plant and animal carbohydrate utilization (left) or the ratio of mucin glycan to plant carbohydrate utilization (right) in the Hadza and Americans. (**D**) Representation of CAZymes in metagenomic data sets related to multiple classes of polysaccharides are plotted by their respective distributions. (**E**) The distributions of Shannon diversities for antibiotic resistance genes (ARGs) across populations identified in metagenomic data. The color key at the bottom of the figure applies to all panels. All boxplot distributions are tested using the nonparametric two-sided Wilcoxon rank sum test with Holm correction for multiple hypothesis testing. Center values indicate the median and error bars, the SD; *$P < 0.05$, **$P < 0.01$; ns, not significant.

In the dry seasons, the Hadza consume more meat, which corresponds with the enrichment of CAZymes related to animal carbohydrate (Fig. 2D; $P = 0.03$, $P = 0.04$, Wilcoxon). Fructan utilization is enriched in the wet season (fig. S4B; $P = 0.02$, Wilcoxon), coincident with berry consumption. Overall, the wet-season Hadza microbiota has fewer plant, animal, and mucin CAZymes compared with the dry- season microbiota (fig. S4B; $P = 0.003$, $P = 0.02$, $P = 0.01$, respectively; Wilcoxon). Analyses of KEGG functional groups that rely on nucleotide sequence similarities showed analogous patterns, including consistent representation across the dry seasons, despite limitations of this approach in identifying novel genetic sequences (tables S3 and S4). Notably, the repertoires of antibiotic resistance genes found in the Hadza were distinct from those of U.S. gut metagenomes (*23*) (figs. S4C and S5) and less diverse regardless of season (Fig. 2E; $P < 0.05$, Wilcoxon), demonstrating that the increased diversity of Hadza microbiome composition does not necessarily result in an enrichment of diversity in all functional classes of genes.

Therefore, data from the Hadza show both enrichment of function for major dietary components across seasons and conservation of function for two sequential dry seasons. We used untargeted metabolomics, a sequencing-independent approach, to generate a high-dimensionality "fingerprint" of community functionality (*26*). These data also perfectly differentiated between the seasons using unsupervised learning methods (fig. S4D) yet did not differentiate between the two dry seasons.

We wondered how our microbiota profiles from the 350 Hadza stool samples that we collected compared with other traditional and industrialized populations. We analyzed compositional data from 18 populations across 16 countries derived from 26 cohorts using taxonomic assignments (table S5). The 18 populations separated along the first principal coordinate corresponding to modernization (Fig. 3 and figs. S1 and S6, A and B).

In addition to the pronounced separation of cultures, there were additional features in the data. First, during the cyclic disappearance of taxa, the Hadza microbiota shifts to a state with increased similarity to those of industrialized microbiotas (fig. S1). Conversely, some OTUs within microbial families common to both traditional and industrialized populations are less seasonally volatile (Fig. 1F and fig. S3, C and D; $P = 7 \times 10^{-13}$, Wilcoxon). Second, the Prevotellaceae, a member of the Bacteroidetes phylum, is a common family in the Hadza microbiota, leading us to wonder about its relationship to the Bacteroidaceae, a dominant family in industrialized populations, which is also a member of the Bacteroidetes phylum. A continuous variable contributing to separation along the first principal coordinate is a trade-off between Bacteroidaceae and Prevotellaceae, consistent with previous findings (*13*, *27*, *28*) (fig. S6, C and D). Thus, industrialized populations have microbiotas

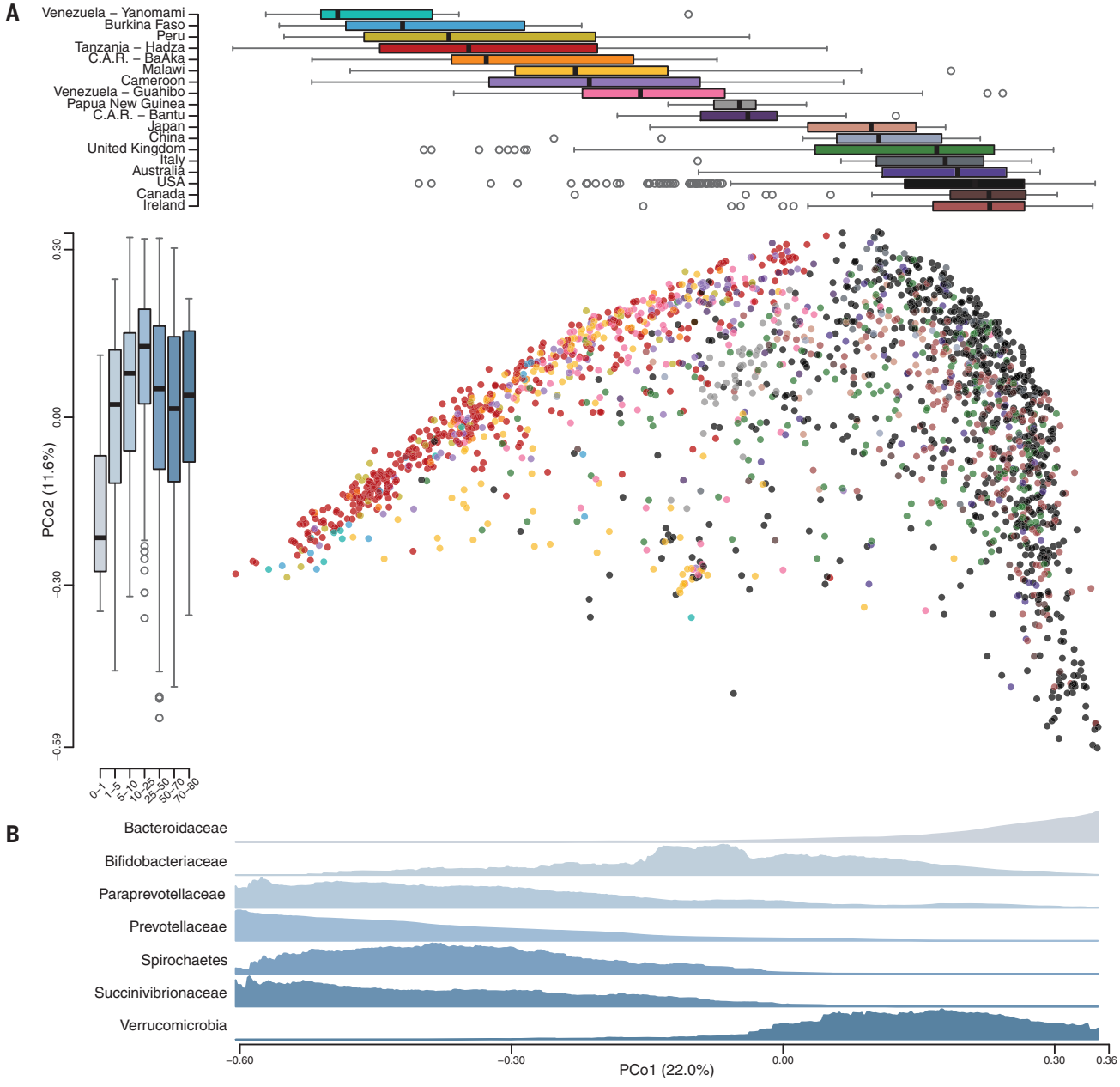

Fig. 3. Gut microbiotas across geography are distinguishable by lifestyle. (**A**) Bray-Curtis dissimilarity PCoA (center panel) based on 2064 microbial community compositions described at the family taxonomic level across populations, including the 350 samples from this study. Each circle represents the placement of a microbial community projected in a subspace that maximizes the variance of the underlying taxonomic data; colors correspond to populations in the top panel. Boxplots (top panel) indicate the distribution of each population along the first principal coordinate (PCo1). The boxplots on the left panel depict the distribution of available ages (indicated in years) according to their gut microbial community placement on the second principal coordinate (PCo2). Boxplot center values represent the median and error bars represent the SD. (**B**) Density plots of seven taxa were generated by using a moving average of the abundance of the families within the communities along PCo1, with a scale from zero to the maximum moving average. These seven families were chosen based on a notable trend along PCo1 or basis in the literature.

that are dominated by Bacteroidaceae (mean 20.9% versus 0.8% in traditional), whereas traditional populations across African, Asian, and South American continents, which include a range of lifestyles from rural agriculturalists to hunter-gatherers, have microbiotas that are in part distinguished by their abundances of Prevotellaceae (mean 29.8% versus 7.6% in industrialized). Third, Spirochaetaceae and Succinivibrionaceae, two prevalent families within the Hadza and other traditional groups, are rare or undetected in industrialized guts ($P < 2 \times 10^{-16}$ and $P < 2 \times 10^{-16}$, respectively; Wilcoxon) (table S5). For example, in one comprehensive study (*13*) of 299 U.S. residents, 15% of the individuals possessed Succinivibrionaceae, with an average relative abundance of only 0.006%, and Spirochaetaceae were undetected in all samples. By contrast, all Malawians and Venezuelans possess Succinivibrionaceae, with an average relative abundance of 3.2%, and 67% of these people harbor Spirochaetaceae at an average relative abundance of 0.6% (fig. S7, A to C). A fourth feature in the data reveals that industrialized guts are enriched in Verrucomicrobia, a group of mucin-degrading bacteria that are rare in traditional populations' guts ($P < 2 \times 10^{-16}$; Wilcoxon).

Together, our data show that in Hadza individuals living a traditional hunter-gatherer lifestyle, the gut microbiota follows a cyclic succession of species that correspond with enrichment of seasonally associated functions. We show that the abundance of many taxa drops below our ability to detect them and then reappears in other seasons. The taxa that are driven to undetectable levels in the Hadza microbiota correspond to taxa that are rare or absent, regardless of season, in industrialized populations. Our observations reveal industrialized microbiome enrichment of mucin-utilizing glycoside hydrolases and the prevalence of Verrucomicrobia, findings that mirror the microbiota response in mouse models deprived of dietary fiber (*29*, *30*). Together, these data indicate the microbiota of many urbanized people is characteristic of a diet limited in the plant-derived complex carbohydrates that fuel gut microbiota metabolism and maintain resident bacterial populations (*12*). Numerous other factors associated with industrialization could also be affecting the microbiota of people from higher-income countries. The challenge is to understand the importance of the ecological role and functional contributions of species with which humans coevolved but that are now apparently underrepresented or missing in industrialized populations.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S8
Tables S1 to S9
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Samuel A. Smits, Jeff Leach, Erica D. Sonnenburg, Carlos G. Gonzalez, Joshua S. Lichtman, Gregor Reid, Rob Knight, Alphaxard Manjurano, John Changalucha, Joshua E. Elias, Maria Gloria Dominguez-Bello and Justin L. Sonnenburg

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Seasonal diets, seasonal microbiota

Among the Hadza of western Tanzania, a few hundred people still live in small groups as hunter-gatherers, reliant solely on the wild environment for food. Smits *et al.* found that the microbiota of these people reflects the seasonal availability of different types of food (see the Perspective by Peddada). Between seasons, striking differences were observed in their gut microbial communities, with some taxa apparently disappearing, only to reappear when the seasons turned. Further comparison of the Hadza microbiota with that of diverse urbanized peoples revealed distinctly different patterns of microbial community composition.

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