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Current views on hunter-gatherer nutrition and the evolution of the human diet

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Abstract

Diet composition and food choice are not only central to the daily lives of all living people, but are consistently linked with turning points in human evolutionary history. As such, scholars from a wide range of fields have taken great interest in the role that subsistence has played in both human cultural and biological evolution. Central to this discussion is the diet composition and nutrition of contemporary hunters and gatherers, who are frequently conscripted as model populations for ancestral human nutrition. Research among the world's few remaining foraging populations is experiencing a resurgence, as they are making the final transition away from diets composed of wild foods, to those dominated by domesticated cultigens and/or processed foods. In an effort to glean as much information as possible, before such populations are no longer hunting and gathering, researchers interested in the evolution of human nutrition are rapidly collecting and accessing new and more data. Methods of scientific inquiry are in the midst of rapid change and scholars are able to revisit long-standing questions using state of the art analyses. Here, using the most relevant findings from studies in ethnography, nutrition, human physiology, and microbiomes, we provide a brief summary of the study of the evolution of human nutrition as it has specifically pertained to data coming from living hunter-gatherers. In doing so, we hope to bridge the disciplines that are currently invested in research on nutrition and health among foraging populations.

KEYWORDS

diet composition, forager, gut microbiome, human evolution, nutrition

1 | INTRODUCTION

Diet composition and food choice are indisputably a core facet in all human societies. Changes in diet are routinely associated with watershed moments in human evolution—such as tool making, brain expansion, family formation, cooperation, and even increased longevity (Aiello & Wheeler, 1995; Lee & DeVore, 1968; Wrangham, 2009). In the not-too-distant past, before industrialization, the rise of the middle class, and the development of market economies, procuring and preparing enough food to feed one's self and one's family occupied a significant portion of daily labor. In contemporary unindustrialized small-scale societies, this is still largely the case (Hawkes et al., 1997; Marlowe, 2010; Wood & Marlowe, 2013). Appropriately, anthropologists take great interest in the role that food and diet have had in human biological and cultural evolution (Messer, 1984). The old proverbs, "you are what you eat" and "tell me what you eat and I'll tell you what you are" (Brillat-Savarin, 1862) speak about food not only as a physical embodiment of the environment, but also as a means of social identity and symbolic construction of culture. Naturally, these are anthropological dialogues, but at their core, they speak the language of many fields of biology. In order for scholars interested in the evolution of the human diet to integrate work from various disciplines, a collective conversation between historical, cultural, biomedical, and nutritional researchers is essential. While each domain certainly has more to say than what can feasibly enter cross-disciplinary communication, it is a necessary endeavor to pull together various lines of evidence used to make claims about the ways in which nutrition informs our understanding of human evolution.

Anthropological investigations on the evolution of human diet can be broadly categorized into two deceptively simple questions of *what* and *how*. *What* types of foods were targeted by our hominin ancestors, and *how* were these foods used to meet nutritional needs in a given dietary ecology—accounting for physiology, technology, and behavior? Ascertaining evidence about *what* was eaten informs the starting point for questions as to *how*, and yet the inquiry of the former is necessarily driven by the latter. Nothing represents this paradox more clearly than the study of contemporary hunters and gatherers, whose diet is often recruited as a reference standard for the evolution of human nutrition (Kelly, 2013; Marlowe, 2005).

Ongoing research among foraging populations is conducted by a wide variety of disciplines, ranging far afield from anthropology. Not only are behavioral and quantitative dietary data collected, but also an array of human biological samples (e.g., urine, stool, saliva, serum, blood, dental calculus, and hair) (Gurven et al., 2016; Leonard, Vashro, O'connell, & Henry, 2015; Pontzer et al., 2012). These samples are then analyzed in an attempt to gain insight into the physiological parameters of various modes of human subsistence. One of the obstacles facing anthropologists is that much of the data generated by studies in nutrition chemistry, human biology, and microbiology are highly technical and rarely take into account how forager health and nutrition is integrated into a larger ethnographic or evolutionary context (Keusch, 2003). Likewise, many anthropologists working with contemporary foragers are often exclusively focused on the ways in which dietary data can be used to inform evolutionary models of human behavior (e.g., food sharing, sexual division of labor, and social network formation) (Hawkes, O'connell, & Blurton Jones, 1989; Isaac, 1978; Yasuoka, 2006).

As the world's foraging populations dwindle, the joint spotlights of scientific inquiry and media fascination have united their focus on obtaining as much information as possible from these small-scale societies. This paper is an attempt to bridge the disciplines that are currently invested in research on nutrition and health among foraging populations. Our aim is to provide a summary of the anthropological study of human nutrition, which is a means for understanding human diet in evolution. We do so by focusing on diet composition, as it has specifically pertained to data collected among living foragers. To do this, we incorporate the most relevant findings from studies in ethnography, nutrition, human physiology, and on **microbiomes**.

2 | NUTRITION SCIENCE AND FORAGER DIET

The field of nutrition science most notably deals with the relationships between food composition, physiology, and disease while nutritional anthropology may be considered a more qualitative perspective on the role that food plays in sociocultural, biological, and evolutionary aspects of the human condition. Their paths have obvious overlap, however, particularly as they pertain to human biological adaptation to nutrition. This overlap is not always appreciated—and this may stem from the fact that nutritionists and anthropologists use different types of data to answer discipline specific problems. Nutritionists are largely concerned with applications in public health, whereas anthropologists may find controlled dietary studies too restrictive, too specific to populations living in the postindustrialized west, and/or not modeled using an evolutionary interpretive framework.

Our ability to apply our knowledge about human diet in evolution towards questions in anthropology, biology, or evolutionary medicine depends on the quality of the information about human forager diets that is available. This means that, in theory, we require detailed dietary profiles of human foraging populations that include not only accurate estimates of how much is collected and consumed, but *also* provide chemical composition data for the foods in question. This type of detailed data is quite rare.

Rather, the literature provides population-specific reports that may or may not outline a systematic process of collecting dietary information. Studies on human foragers over the last several decades have varied greatly in both methodology and depth of dietary focus, stemming from a general lack of standardization in the objectives, methods, or analysis of dietary research. While this is understandable given the wide range of topics that scientists are interested in exploring, the end result is that data collected for one population is not readily comparable to those collected in another. This issue is not new to the field. For the past two decades, scholars have lamented the fact that reproducibility in ethnography is almost impossible (Burch, 1998; Lee, 1992). Even more distressing is that the rate and magnitude of ecological change more recently faced by small-scale societies (in some instances a decade—or less) makes it almost impossible to collect longitudinal or comparable datasets within and between populations

Below, we discuss the criteria for defining a hunter-gatherer, review what we know about the diet composition of foragers based on the present literature, and then outline the most critical issues to consider in future research, both in the field and the laboratory, as they pertain to cross-cultural interpretations of forager diet.

2.1 | What is a hunter-gatherer?

Defining "forager" or "hunter-gatherer" is the first problematic task. For many scholars, the definition is based entirely on subsistence mode and refers to "societies which [. . .] obtain their food and other requirements directly from wild natural sources" (Woodburn, 1980, p. 95), or more specifically the collection of wild plant foods and game animals with "no deliberate alteration of the gene pool of exploited species" (Panter-Brick, Layton, & Rowley-Conwy, 2001, p. 2). While this may appear to be a relatively straightforward classification, it becomes difficult when using this definition to apply to all of the food consumed by a given population. In 1968, it was estimated that the then existing foraging populations (defined as those who consumed 100% of their diet from wild foods) were less than 0.001% of the world's population (Lee & Devore, 1968). In the mid-1990s, it was estimated that of the few remaining hunting and gathering groups, *no* population was consuming an entirely "wild" diet. The criteria for categorizing a foraging population based on diet composition shifted to mean that approximately 10-15% of the diet came from domesticated foods (Kelly, 1995). Today, in the 21st century, if we were to use the criteria that foraging populations must consume a diet of over 90% wild foraged foods, no population would meet the designation (Apicella & Crittenden, 2015). It is, therefore, important for current investigators to acknowledge that in the 21st century, almost all foraging populations consume a mixed-diet that includes varying degrees of farmed foods, wild foods, and possibly nutritional subsidies from governments and aid organizations (Headland & Blood, 2002).

Beyond diet composition, anthropologists are wont to classify foragers using varied measures. Some argue that consideration should be paid to the unique social lives of hunter-gatherers, which includes degree of mobility, group size, and/or kinship systems (Lee, 1992). Some argue for a delineation based on classifying foragers as "generalized" or "immediate return" versus "complex" or "delayed return." Immediate return foragers consume their yield shortly after procurement and delayed return foragers store their food for varying lengths of time (Price & Brown, 1985; Woodburn, 1998). The definitions do not end there. As Lee so aptly states, "Even if it is agreed that hunters and gatherers exist, almost everything else about them is a matter for contestation" (Lee, 1992, p. 31).

Regardless of what distinction or definition is used, contemporary foraging populations continue to be used as the referential standards for inferring evolutionary origins of behavior, health, and diet. While hunter-gatherer studies have waxed and waned in popularity over the last several decades (Lee, 1992), their interest to evolutionary, sociological, demographic, and human health science studies is currently seeing a resurgence, as populations increasingly transition into a wage economy (Headland & Blood, 2002). It is more critical than ever to bridge the gap between anthropology and other biological sciences (e.g., nutrition, microbiology, and energetics), in terms of gleaning the most relevant information on modern forager nutrition that can help in reconstructions of the past.

2.2 | Diet composition

For numerous and understandable reasons, overview nutritional summary papers about contemporary hunter-gatherers are routinely cited as comprehensive and definitive sources of information on forager diet. While valuable, much of these data are taken from anecdotal ethnographic records and, therefore, differ in methodology and the type of information reported. In addition, current dietary models based on summary estimations tend to broadly include or exclude complete categories of food (e.g., dairy, grains, drupes, and legumes). The justification for these dietary restrictions stems from a comprehensive summary paper written by Cordain and colleagues (2000), which was based upon a then forty year old collation of nonstandardized tabulations in ethnically and geographically widespread human populations (Murdock's *Ethnographic Atlas*). While providing a valuable entry point for discussion of variation among foragers from different latitudinal living environments, it has several limitations that are worth noting.

First, the *Ethnographic Atlas* (Murdock, 1967) is a cross-cultural index that is sourced from nonspecialists—largely ethnographers who were not focused on nutritional research. Second, the populations listed in the *Atlas* are categorized by the percentage of their subsistence dependence on categories of foods (i.e., wild plant foods and game meat) —yet no consistent unit of measurement has been used for each instance of data collection. This is explicitly acknowledged by Cordain et al. (2000) and yet, in synthesizing those data, later works underestimated the gravity of this distinction, leading to problematic interpretations, such as claims of a universal prehistoric hunter-gatherer diet. Cordain et al. (2000) state, "Although Murdock did not specify whether the subsistence-dependence categories were based on the energy content or weight of the food for each subsistence economy (gathered plant foods, hunted animal foods, and fished animal foods), examination of the >400 original references indicates that in many cases, estimates were made by weight" (Cordain et al., 2000; 683). As there is no consistency in the units of measurement for each population, some have argued that reliance on the *Atlas* compendium of forager data may be debatable from the outset (Milton, 2000). Furthermore, even if we take the starting point of weight (grams of food) and assume that most studies in the *Atlas* used this unit of measurement, there is no clear indication of how successive authors may select which categories of food to include in their summary and/or how authors may go from field weight (grams) to energy for each specific food. While Cordain et al. (2000) did obtain all of the energy density data from a comprehensive database for wild plant chemical composition (see Brand-Miller & Holt, 1998), it is ecologically limited to species consumed only by Australian aboriginals. Despite these limitations, however, the meta-analysis by Cordain and colleagues provides intriguing data on the ratios of plant to animal contributions and can be used as a starting point to discussion. The extracted data for 229 populations from the *Atlas* suggests that in tundra (circumpolar) environments with limited foliage, meat from hunted or fished animal foods contributes approximately 85% of the diet of the diet. Animal products contribute 42–62% in grassland ecosystems and 52–80% in forests (including temperate and rain forests) (Cordain et al., 2000; 686).

Some nutrition scholars over the past decade have argued that the plant to animal subsistence ratios outlined above overplay the contributions made by animal products and downplay the significance of plant foods in the dietary repertoire of foragers. This may be linked to factors such as the way in which energy estimates were calculated, an observational bias of only attending to men's activities (Slocum, 1975), or due to the inclusion of circumpolar and mounted equestrian foragers[1] (Marlowe, 2010; Milton, 2000). Indeed, alternative compilations of forager diet confirm this position. Both the seminal paper, "Paleolithic Nutrition" (1985), and the subsequent book by two of the same authors, the *Paleolithic Prescription* (1988), were the primary sources of cross-cultural data on forager diet prior to the analysis by Cordain and colleagues. These sources suggest that plants constitute a much higher contribution to the diet, approximately 65%, with animal products making up the remaining 35% (Eaton, Shostak, & Konner, 1988). In addition, a more recent analysis by Frank Marlowe (Marlowe, 2005; and also summarized in relation to the Hadza of Tanzania in his 2010 book, *The Hadza*) suggests that the median diet of warm-climate foragers is composed of 53% gathered plant foods, 26% hunted foods, and 21%

[1]Mounted equestrian foragers tend to have larger home ranges and group sizes, lowered travel costs, and higher rates of hunting success compared to their nonequestrian counterparts (Shimkin, 1983).

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fished foods. This estimate, based on data collations from 179 foraging populations found across several older sources (namely Lewis Binford's *Frames of Reference* and Robert Kelly's *The Foraging Spectrum*), makes the notable contribution of including fished resources, yet no methods of analysis for energy calculations are included—making it difficult to compare with other meta-analyses.

While summary compilations of forager diets, such as those outlined above, do have limitations, they should not be discounted. They provide a valuable overall snapshot of the *range* of contributions made by both plant and animal resources in varied environments (Konner & Boyd Eaton, 2010). Using the combined meta-data from cross-cultural summaries can be useful, but is better contextualized when also incorporating the quantitative nutritional and ecological data from individual hunting and gathering populations.

Population specific dietary data is, however, notoriously difficult to summarize. It ranges from enumeration of food species targeted (Marlowe, 2010), to tallying the number of food units acquired during foraging or consumption (Berbesque, Marlowe, & Crittenden, 2011; Hawkes et al., 1989; O'dea et al., 1991), to estimating whole weights of raw meat or plant foods provisioned to camp (Lee, 1968; Marlowe et al., 2014; Tanaka, 1976, 1980) to quantitative nutritional chemistry of wild food samples (Arnold, Wells, & Wehmeyer, 1985; Miller, James, & Maggiore, 1993; Murray, Schoeninger, Bunn, Pickering, & Marlett, 2001; Schoeninger, Bunn, Murray, & Marlett, 2001). Surprisingly few studies have integrated all of these lines of evidence to provide a comprehensive understanding of forager diet composition, incorporating the nutritional chemistry (i.e., chemical composition of foods), raw weights of food back to camp, and estimated production and consumption patterns (see Altman, 1984; Crittenden, 2009; Hill, Hawkes, Hurtado, & Kaplan, 1984; Hurtado & Hill, 1990; Kuhnlein, Soueida, & Receveur, 1996; Lee, 1969; Wilmsen, 1982). Yet, by pulling together population specific studies and coupling them with what we can glean from summary meta-analyses, it is possible to construct a list of traits that characterize forager diet composition. These include **dietary breadth**, seasonality, and ecological variation.

2.3 | Dietary breadth

The large number of species targeted by foraging populations worldwide has long been noted (Kelly, 2013; Panter-Brick et al., 2001), yet as Hill et al. (1984) state, "Lengthy food lists of all resources ever exploited may be of very limited use in understanding the basic economy of foraging peoples" (Hill et al., 1984, p. 128). Quantifying the number of foods targeted by foragers underscores the speciose nature of a diet based on wild foods, yet it is also necessary to point out that only a small number of the total available resources provide the bulk of forager nutrition. For instance, a comprehensive analysis of the !Kung (or Ju/'hoansi or San) diet revealed that of the 85 total plant species in the diet, only 9 were routinely consumed; of the 54 total animal species available, only 17 were routinely targeted (see Lee, 1968 for original methods and data analysis and Lee, 1980 for an expansion of the nutrition discussion). A detailed list of Hadza foods reveals that while a total of 880 species make up the available resources (both plant and animal), only a fraction of these are routinely consumed (Marlowe, 2010).

Detailed quantitative dietary composition data, including return rates, raw weight of foods (in kilograms), and kilocalorie values of foods, are available for only a handful of populations. Outside of circumpolar regions, where animal products make up the bulk of nutrition (Bang, Dyerberg, & Sinclair, 1980; Draper, 1977; Kuhnlein, Appavoo, Morrison, Soueida, & Pierrot,1994; Kuhnlein et al., 1996), many of the diets are dominated by plant resources. The two most extreme examples are the !Kung, who are reported to have obtained 60–80% of their diet from wild plants when small bands were still foraging full time (Lee, 1968), and the Hadza, who consume approximately 50–65% of their diet from plant foods (Marlowe et al., 2014). It is important to note that these estimates are averaged across seasons and do not take into account differences due to seasonality—which in the tropics, depending on rainfall patterns, can lead to substantial fluctuation in the contribution of plant or animal foods (Marlowe, 2010).

Despite the great dietary breadth that we see across foraging populations, general categories of foods are useful when compiling cross-cultural comparisons. For example, major food groups based on qualitative nutritional characteristics or species traits may include: berries, underground storage organs (e.g., tubers), drupes, gourds, young greens, seeds, and nuts; large and small ungulates, avian game, small land fauna (e.g., lizards and rodents), fish/shellfish, lacustrine or riparian game, insects, larvae, and honey. It should be noted, however, that using general categories might obscure or exclude entire categories of relevant foods. In addition, meat consumed by foraging populations is not limited to large game muscle tissue and extends to all edible portions of the carcass—inclusive of organs, bone marrow, and sometimes even the contents of the gastrointestinal tract of the animal (Buck, Berbesque, Wood, & Stringer, 2015). Furthermore, many populations also consume variable quantities of insects, which until quite recently were often discarded or underestimated (Bodenheimer, 1951; McGrew, 2014), and can provide substantive nutrition in some populations (Crittenden, 2011; Marlowe et al., 2014). Seasonality, as noted above, is also a critical factor in making claims about diet composition in any ecological setting.

2.4 | Seasonality

Anthropologists have long acknowledged the importance of seasonality on both ecology and behavior. Seasonal variation influences, and is influenced by, not only rainfall patterns and availability of resources (Hart & Hart, 1986; Speth & Spielmann, 1983; Ulijaszek & Strickland, 2009), but also diet composition (Altman, 1984; Kitanishi, 1995; Speth, Widdowson, Oftedal, Foley, & Van Soest, 1991), and food sharing (Speth, 1990), group composition and residence patterns (Thompson, 1939; Woodburn, 1968), work-load (Hurtado & Hill, 1990), sleeping patterns (Ingram & Dauncey, 2009; Samson & Nunn, 2015), and even ritualistic behaviors (Ulijaszek, 2009). Despite this acknowledgement, most discussions of forager diet overlook seasonal variation (see discussion by Hurtado & Hill, 1990). The imperative point is for anthropologists collecting nutritional data among foragers to consider the importance of seasonality when collecting data in the field—and to attempt to address any seasonal variation when using summative data from the literature.

2.5 | Ecological variation

Over the past several decades, scholars focused on forager nutrition have increasingly stressed the importance of ecological variation (Kelly, 2013; Kent, 1996). There is no *one* hunter-gatherer diet (Konner & Boyd Eaton, 2010). As more data accumulate, it is abundantly clear that no trans-geographical and trans-cultural forager diet compendium exists. As Speth so succinctly states, "Not surprisingly, as our data base on hunter-gatherers improves, anthropologists are also finding significant differences between groups" (Speth, 1990, p. 151).

Anthropologists working among the world's few foraging populations have not maintained a fixed position that hunter-gatherers represent Stone Age populations. Rather, most ethnographers, as well as evolutionary anthropologists and behavioral ecologists, recognize that while foragers are not analogs to the Paleolithic past, their small population size and nomadic lifestyle—in the absence of agriculture—makes them a useful tool for expanding our understanding on the evolution of human behavior. The discipline has also moved forward with the tacit acknowledgement that, despite coexisting with farmers and horticulturalists for extended periods of time (sometimes centuries), foragers have been able to continue their hunting and gathering way of life (Lee, 1992). Looking to why and how foragers have been able to continue their subsistence economy has increased our appreciation for geopolitical history as well as ecological variation (Marlowe, 2002).

2.6 | Methodological/analytical considerations

2.6.1 | Units of measurement—weight versus energy

The majority of studies that provide dietary estimates of food type contribution use either mass (e.g., gram) or energy (e.g., kilocalorie) units. Interpretations of diet based upon the contribution of a food item to total diet per unit mass versus per unit energy will lead to wildly different perceptions about the value of that food item (e.g., honeycomb may weigh far less than a particular plant food, but it contains far more energy per unit mass). Furthermore, it is rarely noted whether the weight of a food is reported as **wet weight** or **dry weight**. This is critical, as the percent of water in any given food can greatly alter its mass and its mechanical fracture properties, which impact tissue displacement and nutrient release from cells (Wollstonecroft, 2008). Further complicating the issue in estimations of energy derived from meat is **drip loss**, which can greatly reduce the raw weight of muscle tissue and potentially the amount of surface fat (Honikel, 1987). While it might not be possible to accurately estimate drip loss from cooking or, for instance, starch access in an aqueous matrix (Tydeman et al., 2010), researchers can be aware that they might be overestimating the contributions of meat and plant **carbohydrates** to the diet when using variations of raw or dry weight estimates.

It is also very often unclear whether researchers outside of nutrition science are using the standard unit in nutrition of **kilocalories** (kcal) per gram (kcal/g). Many nonnutritionists use the abbreviated term "calorie" —which is problematic for the following reasons.

The first issue is that 1 kcal is equivalent to 1 **Calorie** (see **large Calorie**) and 1000 calories (see **small calorie**). For reference, 1 small calorie is equivalent to approximately 4.2 **joules (J)**.[2] In the context of human energetics, it is most appropriate to use the metric factor of "kilo" for kcal and **kilojoule** (kJ), because energy content of food and energy expenditure of the human body operate at these unit quantities. For example, human daily resting energy expenditure is approximately 6720 kJ (6,720,000 J) or 1,600 kcal (1,600,000 calories) per day (Passmore & Durnin, 1955). The second issue with using the term "calorie" is that while it represents the most familiar unit of food energy to consumers in the US, it is etymologically inaccurate. Instead, the word "Calorie," with a capital "C," technically equates to kilocalorie, and was abbreviated in the late 1800s based on the **Atwater system** of food energy conversion (Atwater, 1894). By the early 20th century, the word "calorie," irrespective of capitalization and colloquially referring to kilocalorie, was already in widespread use in both nutritional policy and the public (Hargrove, 2006). This has led to misuses and misunderstandings of food energy units and their abbreviation, where the misleading abbreviation "kCal" (which would technically mean 'thousand-thousand calories') is often used instead of "kcal," owing to the misunderstanding of the meaning of "calorie" and "Calorie" (see glossary). Some nutritionists have begun to urge researchers to move away from the use of kcal completely — and adopt the international standard of kJ (Hargrove, 2007).

The issue of measuring food energy is particularly problematic when using ethnographic data that do not provide a unit of measurement. The solution when comparing cross-cultural data is to do the following: (a) evaluate the primary data set for units (e.g., gram versus kilocalorie), (b) determine whether wet weight or dry weight is being reported and standardize the usage across reports, and (c) use appropriate mass to energy conversion references for cooked or raw weights when possible. Moreover, all researchers conducting field nutritional studies should provide a step-by-step explanation of how they acquired raw weights *in the field* (e.g., directly measured with a scale or approximated against an explicitly-defined mass/volume referent) and how these raw weights were converted to energy estimates. The following example illustrates one such approach for acquiring and reporting nutritional data beginning with field measurements:

Field measurement to edible weight:

1. Obtain the raw wet weight (g): scale measurement (g) of raw unmodified food resource
2. Obtain the edible wet weight (g): raw wet weight (g) with inedible or discarded portion (g) subtracted
3. Obtain the edible dry weight (g) if possible: edible wet weight (g) with **moisture content** subtracted

[2]The "joule" is named for James Prescott Joule (Hargrove, 2006) and, as such, the first letter of its symbol is the upper case letter "J" (J). When spelled out in English, however, the standard practice using the International System of Units (SI) is to begin with a lower case letter, as in "joule".

Edible weight to energy (kcal/g):

1. For published dry weight food energy values, listed as "kcal/g": edible dry weight (g) × kcal/g dry (cite publication source that is being used for kcal estimate)
2. For published wet weight food energy values, listed as "kcal/g": edible dry weight (g)/(100 − % moisture) × 100 × kcal/g wet (cite publication source that is being used for kcal estimate)

An example of field measured wet weight to final energy calculation using dry weight estimations is as follows:

Step 1: 1500 g of //ekwa tuber measured in the field with a hanging spring scale.

Step 2: Based on Schoeninger et al. (2001), the range of inedible fraction for this species of tuber is 25–79%. If we use 25% inedible fraction, 1125 g of the original sample is edible fresh weight.

Step 3: Based on Vincent (1985), this species of tuber has an average moisture content of 70%. Removing water (1125 g × 0.70 = 787.5 g; 1125–787.5 g), 337.5 g of the original sample is edible dry weight.

Step 4: Multiplying the calculated edible dry weight of the sample, 337.5 g, by the published kcal per gram dry weight estimate in Schoeninger et al. (2001), 2.79 kcal/g, the original sample of 1500 g yields approximately 942 kcal.

While this represents only one example of how foods can be converted from field weight to energy, it illustrates the number of steps that are necessary in order to achieve transparency and standardization of methods.

2.6.2 | Wild versus domesticated foods

It is often difficult to obtain reliable or consistent values for macronutrient content of wild foods. Wild game meats, for example, are lower in saturated fat and provide moderate to high protein as well as higher shares of **monounsaturated** and **polyunsaturated fatty acids** when compared to meat from domesticated animals (Mann, 2000; Onyango, Izumimoto, & Kulima, 1998; Talbot, Payne, Ledger, Verdcourt, & Talbot, 1965). Plant foods are even more problematic. Samples that have been collected in the field and subsequently analyzed in a nutrition lab often have no consistent composition because they vary in size (as they are not domesticated), and are likely to have a wide discrepancy in water content (Miller et al., 1993). This results in extremely high standard deviation values for repeat measurements, even when subsampling the same specimen. Foragers consume plants in various stages of desiccation and maturity—and, depending on when the plant sample was collected (ripe vs. unripe), the water and nutritional content will vary.

The solution to these issues is to use wild variants of the species as a nutritional reference, if possible. If unavailable, the best practice is to use nutrition values for the most closely related species, while taking care to report the botanical names (*Genus species*) of the reference and wild food specimens whenever possible. This allows future generations of researchers to identify botanical samples that can then be analyzed in the laboratory, thereby adding to the corpus of wild food compositional data available.

2.7 | Fiber content and analysis

The fiber content of wild foods is often another problematic area within the broad subject of forager nutrition research. There are two areas of confusion: definition and measurement. The first point of confusion is due to the fact that there is no singular definition of fiber beyond the notion that it is a type of largely indigestible carbohydrate that has certain health benefits[3] such as reduced risk of chronic diseases (Aune et al., 2016), increased gut motility, reabsorption of bile acids, and enrichment of colonic **microbiota** (Anderson et al., 2009; Lattimer & Haub, 2010). Some definitions refer to functional properties (like **soluble fiber** vs. **insoluble fiber**), while other definitions focus on structural properties, such as the nondigestible constituents of plants (Cummings, 1984; Fuller, Beck, Salman, & Tapsell, 2016). Most fiber escapes digestion in the small intestine and is passed into the large intestine (colon). Until quite recently the convention was that insoluble fiber, by definition, does not dissolve in water and is not fermented in the large intestine, whereas soluble fiber, after passing through the small intestine, is then fermented in the large intestine by resident gut microbiota (Flint, Bayer, Rincon, Lamed, & White, 2008; Martens et al., 2011; Stephen & Cummings, 1980). Since this convention is no longer viewed as accurate, nutritionists now argue that the categorization of soluble versus insoluble fiber is not nearly nuanced enough.

First, using the categories soluble/insoluble and prioritizing functional properties overlooks metabolism in the large intestine. Some fibers categorized as "insoluble" are, in fact, fermented in the large intestine and some fibers categorized as "soluble" have no clearly delineated health effects (Lunn & Buttriss, 2007). Second, the narrow classification of soluble/insoluble fiber and focus on structural versus nonstructural molecules often excludes other indigestible components, such as **resistant starches** and **oligosaccharides**. There has recently been a call to action to expand the definitions of fiber that are used by the American Association of Cereal Chemists (AACC), the Food and Nutrition Board (FNB), and the Food and Agriculture Organization/World Health Organization (FAO/WHO) (Lunn & Buttriss, 2007). By differentiating **dietary fiber** from **functional fiber**, the range of nondigestible carbohydrates in the food supply is acknowledged (Slavin, 2013), thereby providing a more accurate distinction. Many nutritionists now argue that clearly identifying different types of fiber, and their roles, is key to moving the field of food science forward (Hutkins et al., 2016).

An additional complicating issue, beyond defining fiber, is its measurement in foods and the estimation of food energy values. While there are a wide variety of experimental protocols, many early methods in traditional dietary analysis and food composition studies excluded

[3] It should be noted that from an evolutionary standpoint, dietary fiber is not always a net positive to human consumers. It is difficult to digest, reduces the energetic value of food, can speed intestinal transit times that limits digestive enzyme activity, and can inhibit absorption of micronutrients, particularly minerals (Harland, 1989; Milton, 1984; Reddy et al., 1999; Stahl, 1989; van het Hof et al., 2000).

fiber from energy calculations (i.e., kilocalorie estimations). In models using the simplified method of "subtraction" or "difference," the measured fat, protein, ash, and water are subtracted from the total weight of the food sample. This difference, the estimated net carbohydrate contribution, is the sum of the nutritionally available carbohydrates (like **starches** and **sugars**), the absorptively unavailable carbohydrates (like **hemicellulose** and **cellulose**), and chemically inert-carbohydrates (like lignin) (Lunn & Buttriss, 2007). The end result of this type of nutritional analysis is that the amount of carbohydrates directly available to the consumer energy pool is often overestimated.

Further adding to the complexity of fiber analysis is fermentation. Some types of dietary fiber that pass into the large intestine are fermented by gut microbiota residing in the colon that produce **metabolites** such as **short chain fatty acids** (SCFA), along with gases and organic acids, and recycle energy back to the human body (MacFarlane & MacFarlane, 2003; Schwiertz, Lehmann, Jacobasch, & Blaut, 2002). More recent nutritional chemistry methods subtract structural carbohydrates (fiber) in the final calculation of caloric content, and the "nutritional carbohydrate" is thus again determined by difference. Recognizing that different types of fiber are metabolized or fermented during digestion and, therefore, have energetic contributions to metabolism will alter estimations of the caloric value of plant based foods. How much energy is made available to the host, however, is debated and difficult to estimate (den Besten et al., 2013; Miller et al., 1993). Estimates on the contribution of SCFA range between 7 and 10% of the daily energy requirements of the host (Cummings & MacFarlane, 1991; den Besten et al., 2013).

While older methods of fiber quantification used nonenzymatic-gravimetric analyses, such as **crude fiber** analysis and **neutral detergent fiber analysis**, there is a call to use more accurate methods to measure carbohydrate content and capture fermentation, such as **enzymatic-gravimetric** methods (for a comprehensive list of various methods of fiber analysis, see Lunn & Buttriss, 2007).

The solution to solving the complex issue of fiber estimation in forager diets is to be clear on what definition of dietary fiber is being used and to review the methods of nutritional analysis/chemical composition being utilized. If the total energy (kilocalories) estimate under question was analyzed by simplified subtraction method, this should be noted, as it is likely an overestimate of nutritionally available carbohydrates. Future laboratory research analyzing wild foods should strive to use enzymatic-gravimetric methods that will directly measure different fiber types and more accurately measure all available carbohydrates. Fiber will continue to be central to the discussion of forager nutrition, not only because it is has been implicated as a key component of the evolution of the human diet (Conklin-Brittain, Wrangham, & Smith, 2002), but also because new trends in microbiome research are exploring the connection between fiber and the composition and function of gut microbiota (Gibson & Roberfoid, 1995; Milton, 1984; Schnorr et al., 2014; Sonnenburg & Sonnenburg, 2014; Sonnenburg et al., 2016; Tap et al., 2015). This necessitates managing not only our definitions of dietary fiber, but also **prebiotic** and **probiotic**. Fiber also has implications for **bioavailability** and how difficult-to-digest plant compounds affect human metabolism. Research on bioavailability of nutrients and food processing technology is an important means for understanding how human diets, past and present, can be based primarily (>50%) on wild plant foods when animal resources are less available.

3 | BIOAVAILABILITY AND HUMAN DIGESTIVE PHYSIOLOGY

Directly addressing the links between bioavailability and digestive physiology alters the course from thinking about foods exclusively as intact but biologically inert specimens, to fractionated but metabolically active substrates. This is important because the accessible portion of food, rather than its total composition, actually determines its biological value. A major part of understanding the evolution of human nutrition is explaining how we developed such large brains with such small guts. Therefore, it stands to reason that we should know the degree to which foods across the panoply of human diets are susceptible to human digestion. In this section, we introduce the concept of bioavailability, outline the basics of human digestive physiology in comparison to great apes, and discuss two major factors that affect bioavailability, particularly of plant foods: gut microbiota and food processing.

3.1 | Bioavailability

The term bioavailability was originally used to refer to the rate and extent that a compound reached the site of activity (Stahl et al., 2002). Until recently, it was a term that exclusively applied to the field of pharmacology, but nutritional sciences adopted the concept and has fostered its broader application in understanding how **micronutrients** and **macronutrients** are incorporated into human tissues (Stahl et al., 2002). Currently the definition has relaxed to a more quantitatively tenable measurement of the fraction of a compound that may be absorbed into systemic circulation (Schumann et al., 1997).

Redefining the concept of bioavailability for nutritional sciences has resulted in the development of a more appropriate term, **bioaccessibility**, which is defined as the portion of a substrate that is made available for absorption (Stahl et al., 2002). Strictly speaking, to measure bioavailability, one must harvest blood serum and analyze the presence of exogenous substances that were absorbed from the gut after digestion. Instead, bioaccessibility is a much more practical assessment of the digestibility of a food. It specifically measures the digestively resistant attributes of food, rather than the more complicating interactions between food constituents and host endocrine or epithelial functions. A basic survey of human feeding and gut morphology informs us of its unspecialized nature, which is itself indicative of a broad systemic requirement for high quality (i.e., nutritionally and calorically dense) foods that are rapidly consumable and digestible (Milton 2000). Therefore, bioavailability or bioaccessibility of a food is an important factor to consider when speaking about dietary and environmental ecologies in human subsistence.

3.2 | Digestive physiology and gut microbiota

The anatomy and physiology of any organism in large part reflects its dietary adaptations and feeding strategy. While this is certainly not a universal rule (Milton, 1987), and primates in particular demonstrate wide variation in dietary niche exploitation, it does suggest that gut function may be broadly equitable across the primate order (for notable exceptions see Chivers & Hladik, 1980; Milton, 1987). Humans and great apes, for instance, share a similar gut morphology: a simple acidified stomach, small intestine, cecum, and colon. Despite these gross similarities, there are a few fundamental differences that separate the human digestive tract from that of other related primates: a reduction in the size of the colon and an enlargement of the small intestine relative to the overall size of the gut (Aiello & Wheeler, 1995; Milton, 1987). Therefore, we can assume a certain baseline level of gut function in primates, particularly humans, for whom the gut is considerably simplified and prioritizes nutritional digestion and absorption in the small intestine.

Humans have experienced a reduction in colon volume relative to the other great apes and, therefore, a greatly reduced capacity to consume and digest high quantities of fibrous or difficult-to-digest foods (Milton, 1987, 1999; Popovich et al., 1997). Despite this, humans are also incapable of rapid passage of ingesta typical of a carnivore-like digestion pattern (Milton, 2000). Chimpanzee diets include, on average, 33.6% fiber (Conklin-Brittain et al., 2002), whereas the minimum recommendations for fiber consumption in modern human diets are only 20–30 g, or about 6% of kcals consumed for a 2000 kcal diet (Papazian, 1997). Digestive rate, along with differences in the gut proportions for humans relative to other great apes (high-volume small intestine and low-volume colon), clearly indicate that the human dietary strategy shifted at some point in our evolutionary history away from processing copious amounts of low-quality, nonfermentable, fibrous plant foods, and instead focused on higher quality, easily digestible, and easily fermentable food.

Early work in the 1980s by Katherine Milton on digestive physiology and kinematics in primates (Milton, 1987; Milton & Demment, 1988) was perceptive in its recognition that not only is the gut a bottleneck to nutritional acquisition for all mammals (Chivers & Hladik, 1980), but also that intestinal microbiota enhance the nutritional value of resistant foods, even in the relatively unspecialized human gut. Notably, Milton and Demment (1988) found that humans are similar to great apes in the capacity to digest and ferment high concentration (10–15%) **neutral detergent fiber** and to degrade cellulose and hemicellulose via fermentation. Several factors, which may vary by instance, affect this process. These include rate of passage through the gut, particle size, food source, and fiber content of food (Cummings, 1984). Unlike ruminants, humans and great apes are inefficient degraders of highly fibrous foods containing lignin, such as grass, **monocot** cereal fibers, or plant fibers (van Soest, Foose, & Robertson, 1983). Instead, relatively fibrous foods without lignin, such as from dicotyledenous vegetables (or **dicots**) like cabbage or carrots, are more compatible with human digestive physiology and gut microbiota (Bergman, 1990; van Soest et al., 1983).

The human gut contains many microbial species that function as primary degraders, meaning that they are efficient metabolizers of dietary cellulose and hemicellulose (but nowhere near as efficient as ruminants) (Flint et al., 2008; Milton & Demment, 1988; van Soest et al., 1983). Additionally, humans (as well as many other animal taxa, including the great apes) harbor a contingency of microbial **cross-feeders** that consume hydrogen (H_2), which is produced in excess during primary fermentation. However, as H_2 is produced, it must be removed so as not to inhibit further fermentation. Humans, as well as many other animals, accomplish H_2 removal mainly by the presence of microbial **methanogens** (archaea) in the gut that convert H_2 to methane (CH_4), which is essentially a waste product (Bergman, 1990). This fermentative process, while fast, is less energetically efficient (due to the production of CH_4 waste), but may be offset by either (1) continuous feeding, which is the strategy of animals that consume low-quality forage, or (2) consuming higher quality and rapidly fermentable foods (Flint et al., 2008; Lambert & Fellner, 2012). The latter strategy best characterizes the dietary scenario for humans and frugivorous primates.

The main reason that this distinction is relevant has to do with the rate of passage of digesta. Passage rate influences the types of microorganisms that can adhere and grow within the gut (Koropatkin, Cameron, & Martens, 2012), and the microbial communities, in turn, determine the primary and secondary metabolite production strategies. Curiously, the volatile fatty acids (SCFAs) produced from fermentation are readily absorbed by the epithelia (the intestinal cell wall) in the lower digestive tract at remarkably similar rates in all mammals, regardless of gut morphology (Bergman, 1990). Therefore, despite reductions in size, the human colon is capable of rapid fermentation and metabolite production, provided the diet is not heavily comprised of nonfermentable carbohydrates like lignin (Milton & Demment, 1988). Coupled with efficient metabolite absorption by the epithelia, humans appear well adapted to digest, ferment, and absorb calorie dense foods (relative to low calorie forage consumed by other great apes) in a sort of high-throughput intestinal digestive system.

3.3 | Food processing and cooking

Food processing, a critical and universal trait of modern human subsistence (Stahl, 1989), is an important factor when considering the nutritional and biological value of foods to human consumers. A formal definition of food processing is dependent on the application at hand. **Industrial food processing** refers to the transformation of raw animal, vegetable, or marine materials into intermediate foodstuffs or edible products through the application of labor, machinery, energy, and/or scientific knowledge (Connor & Schiek, 1997). To accommodate preindustrial, noncommercial, and even nonhuman activities, anthropologists must be cognizant of intentionality. We, therefore, propose the following definition of **traditional food processing** that is more useful for nutritional and evolutionary anthropological investigations of diet: the purposeful external modification of a resource to change its physical or chemical attributes in preparation for consumption. Some modern forms of processing, accomplished with mechanized technology, include grinding, homogenization, pasteurization, defatting, liquefaction, and emulsification, among many others (Connor & Schiek, 1997). In contrast, traditional food processing can often accommodate these same objectives using nonmechanized technological methods, which have been practiced for thousands of years, such as fermentation, germination, mechanical processing, thermal treatment, dehydration, and preservation (Fellows, 2009; Frink & Giordano, 2015). It may be premature to ascribe processing as a uniquely human trait when tool-use and food handling are observed across a wide range of animal taxa (e.g., Apidae, cephalopods, corvids, and procyonids) (King, 1986; Shumaker et al., 2011), yet the operational leap to intentional post-harvest modification is, thus far, restricted to the human lineage (Harmand et al., 2015; Wrangham & Conklin-Brittain, 2003). Since tool use is commonly seen with members of *Pan* (Goodall, 1986; Hernandez-Aguilar, Moore, & Pickering, 2007), it is very likely that early hominins were able to utilize sophisticated tools for extractive foraging (Crittenden, 2011; Lemorini et al., 2014; Milton, 1984; Panger, Brooks, Richmond, & Wood, 2002; Revedin et al., 2010), and engaged in intensive niche construction (Wollstonecroft, 2011). As a result, food processing had evolutionarily relevant consequences that have altered selection pressures on human digestion. This is evidenced by modern human reliance on food processing, particularly cooking, to initiate an externalized phase of digestion and alter the nutritional quality of foods (Carmody & Wrangham, 2009; Stahl, 1984, 1989).

Prior to entering the upper gastrointestinal tract (GI tract), foods are orally comminuted (i.e., reduced to small particles), and this cost of chewing is an oft unappreciated hurdle for human nutritional acquisition (Dominy, Vogel, Yeakel, Constantino, & Lucas, 2008). Particle size reduction, as well as molecular structure disruption that is achieved through cooking, significantly improves salivary amylase activity during chewing (Hardy, Brand-Miller, Brown, Thomas, & Copeland, 2015; Hoebler et al., 1998; Hoover & Vasanthan 1994). This is achieved by exposing enzyme **binding sites** and increasing particle surface area relative to volume. Efficient mixing and exposure to acids in the stomach is also aided by particle size reduction, and peristaltic movement of the ingesta through the small intestine proceeds at a constant and controlled rate in the absence of clumping (Schnorr, Crittenden, Venema, Marlowe, & Henry, 2015). Therefore, even a high quality plant-heavy diet (which may have characterized most hominin diets in subtropical ecologies) must have posed insurmountable barriers to adequate nutritional provisioning prior to external mechanical food processing techniques (Dominy et al., 2008; Zink, Lieberman, & Lucas, 2014), or more advanced technology such as cooking (Carmody & Wrangham, 2009).

Heat reduces the physical structure of complex nutritional and structural components of plants, including starch, **inulin**, cellulose, and **arabinoxylans** (Stahl, 1984; Wandsnider, 1997), making their basic nutritional elements, **monosaccharides**, and oligosaccharides, more digestible (Roberfroid, 1999). Of note is the effect of heat and moisture on semicrystalline starch grains, which are polymers of **amylose** and **amylopectin**. Heating beyond a certain temperature, typically $\geq$50-60° C, in the presence of moisture reduces the integrity of the semicrystalline structure and allows water molecules to enter the starch, eventually dissociating its polymers and bursting the granule in a process called **gelatinization** (Hoover & Vasanthan, 1994). Since gelatinized starch has exposed amylose, this makes it much more susceptible to digestion by amylase enzymes from human saliva or pancreatic fluid (Butterworth, Warren, & Ellis, 2011). Due to the importance of food processing to human metabolism and health, many investigators have advocated for more research on contextually informed models of processing technologies, particularly cooking, to empirically evaluate their benefit to human consumers (Messner & Schindler, 2010; Schnorr et al., 2015; Schnorr, Crittenden, & Henry, 2016; Wollstonecroft, Ellis, Hillman, & Fuller, 2008; Zink et al., 2014).

Currently, only a few studies have sought to directly address the impact of cooking on digestibility from an ethnoarchaeological perspective, and the results are mixed. By feeding mice diets of cooked or raw tubers and meat, Carmody et al. (2011) found that consumption of cooked foods resulted in positive changes in body mass. Similarly, work on pythons found that cooked meat reduced digestion-specific costs, such as **diet induced thermogenesis** (DIT), compared to raw meat (Boback et al., 2007). However, in an attempt to replicate results on mice, Cornélio, de Bittencourt-Navarrete, de Bittencourt Brum, Queiroz, and Costa (2016) found that weight fluctuations were similar regardless of cooked or raw feed. Further work modeling cost of chewing (Zink & Lieberman, 2016) and digestive bioaccessibility (Schnorr et al., 2015) also do not support the conclusion that cooked foods offer a marked improvement in energy availability. These equivocal conclusions warrant further study into the impact of cooking on human nutritional acquisition. In particular, researchers should develop models that are sensitive to culturally- and ecologically-specific food preparation traditions (Capparelli, Valamoti, & Wollstonecroft, 2011).

4 | FORAGER NUTRITION, HEALTH, AND HUMAN BIOLOGY

The disciplines of biological anthropology, human biology, and behavioral ecology have been collecting biological, medical, anthropometric, and nutritional data among living foragers for the better part of the past sixty years. The majority of the early studies were aimed at either capturing disease pattern data to test the so-called **mismatch hypothesis** (Cordain et al., 1998; Eaton, Konner, & Shostak, 1988; O'Keefe & Cordain, 2004; Price, 1939) or at collecting nutritional and health status data as foraging populations transitioned to a more sedentary lifestyle and food economy (Bronte-Stewart, Budtz-Olsen, Hickley, & Brock, 1960; Walker, Sugiyama, & Chacon, 1998). Briefly summarized, the mismatch hypothesis, originally proposed in the 1980s, argues that humans are adapted to our past environment—nutritionally, ecologically, genetically, and perhaps even socially and cognitively (Barkow, Cosmides, & Tooby, 1992; Eaton & Eaton, 2003; Nesse, Stearns, & Omenn, 2006)—and, therefore, we are essentially "stone-agers living in the fast lane" (Eaton, Konner, et al., 1988) and are a "mismatch" with our Paleolithic past (Cordain et al., 1998). The most outspoken proponents of this perspective argue that civilization has essentially outpaced natural selection and created an environment that is not conducive to human biology and adaptation (for review, see: Johnson, 2015; Turner & Thompson, 2013; for critiques, see: Pitt, 2016; Zuk, 2013).

Our aim is not to review the myriad publications that address the mismatch hypothesis using forager health data to discuss the discordance model, the epidemiological transition, or prevalence of diseases of civilization (e.g., obesity, diabetes, cardiovascular diseases, Crohn's disease, irritable bowel syndrome, and cancer). Rather, we aim to review the quantitative studies of health and nutrition collected among living foraging populations. It is outside the purview of this review to discuss the large and impactful body of bioarchaeological literature on health and nutrition changes in skeletal populations undergoing dietary transition. For review, see Armelagos and Cohen (1984), Mummert, Esche, Robinson, and Armelagos (2011), and Roberts and Manchester (2007). The quantitative studies that we focus on below were undertaken among living foragers—both historic and contemporary. They can be broadly grouped as biological/bio-medical research, including anthropometric examinations (e.g., body size and growth), measurements of nutritional deficiencies (e.g., iron deficiency anemia), and oral health investigations (e.g., caries rates and periodontal disease).

4.1 | Anthropometry

Several comparisons of anthropometric measures have been conducted among foraging populations or populations recently settled. As a proxy for nutritional status, most studies directly measured body mass index (BMI), mid-upper arm circumference (MUAC), and skinfold thickness.[4] The data, while collected using similar methods, yielded differing results—making them difficult to assess across populations. Anthropometric comparison between !Kung foragers in transition with settled Kavango horticultural pastoralists in Namibia indicate that the move from nomadic foraging to settled village life had deleterious effects on nutrition status for the !Kung (Kirchengast, 1998). Significant pathogen loads and high levels of alcoholism have also been implicated in transition studies of iron status among the !Kung (Kent & Lee, 1992). Data collected among the transitioning Agta of the Philippines indicates that approximately 34% of adults and 17% of children were malnourished at the time of measurement (De Souza, 2006). It should be noted, however, that the Agta were already transitioning away from a full time foraging economy by the early 1990s (Griffin, 1996) and had sustained trade relationships with neighboring populations for decades prior to transition (Peterson, 1981).

Alternatively, data from the BaAka foragers of the Central African Republic, also collected during transition from the bush to a more settled village life, indicate that despite drastic differences in hematological markers of nutrition between foraging and settled communities, anthropometric measures of nutritional status were not significantly different between populations (Remis & Jost Robinson, 2014). Interestingly, while the group level means before and after transition were not significantly different, sex differences in skinfold thickness and MUAC emerged, showing a distinct pattern between villages (Remis & Jost Robinson, 2014). The authors concluded that these differences in anthropometric variables may be indicative of future health disparities between villages. BMI, however, was not significantly different between the sexes—before or after transition (Remis & Jost Robinson, 2014). These results are consistent with other egalitarian foraging populations, such as the Hadza of Tanzania (Sherry & Marlowe, 2007) and the Baka of Cameroon (Yamauchi, Sato, & Kawamura, 2000). In both cases, BMI between men and women was not significantly different. This may be due to the fact that food sharing patterns in egalitarian subtropical foragers may serve to buffer the energetic costs of reproduction and differential access to resources (Ivey, 2000).

Taken together, the anthropometric assessments of foraging populations in transition broadly suggest that introducing a diet dominated by domesticated cultigens has unclear (but often negative) health effects for the populations under question.

4.2 | Nutritional status

Strikingly few quantitative studies on measured nutritional status of populations in transition have been done. Those that exist have largely focused on micronutrient deficiencies (e.g., iron, zinc, copper, folate, vitamin A, vitamin B12, and vitamin C).

Micronutrient deficiencies have been measured in transitioning foragers since the 1960s. Comprehensive data among subtropical foragers is available for the !Kung (San), the Aka and BaAka of the Central African Republic, the Efe of the Democratic Republic of the Congo, and Australian Aboriginals. Among the !Kung foragers, nutrition status for iron, zinc, copper, folate, and B12 was well within the healthy ranges for men and women across their lifespan before settlement in the 1960s (hematological data: Metz, Hart, & Harpending, 1971; hair samples: Baumslag & Petering, 1976). After settlement, approximately fifteen years later, high rates of iron deficiency anemia were reported (Fernandes-Costa et al., 1984). Several comparable studies conducted among the Aka and BaAka of the Central African Republic found similar results. Aka and BaAka living in more urban settings showed evidence of iron deficiency (Cordes & Hewlett, 1990; Pennetti, Sgaramella-Zonta, & Astolfi, 1986). In a direct comparison of rates of iron deficiency anemia, 15.6% of BaAka women evinced low hemoglobin values in the mid-1980s before transition to village lifestyle (Pennetti et al., 1986), compared to 63% post transition (Remis & Jost Robinson, 2014). Finally, Efe foragers in transition were found to exhibit fewer clinical signs of malnutrition when compared with their horticulturalist neighbors, the Lese (Dietz, Marino, Peacock, & Bailey, 1989). Likewise, similar patterns emerged among aboriginal Australians who transitioned from a traditional foraging economy to a more settled village lifestyle in Aboriginal Lands Trust communities. Before transition, populations consuming a diet composed of predominantly wild foods had low levels of micronutrient deficiencies (O'Dea, Naughton, Sinclair, Rabuco, & Smith , 1997), compared to post-transition, where the sample population was characterized by micronutrient deficiencies in folate, iron, and vitamins A, E, and B12 (Davis, Smith, & Curnow, 1975; Kamien, Nobilet, Cameron, & Rosevear, 1974; Kamien et al., 1975). More recent data on dietary transition now point to increased rates of insulin resistance, diabetes, obesity, and cardiovascular risk (Cameron et al., 2003;

[4]Addressing additional research specifically aimed at growth trajectories of pygmy populations is outside of the scope of the current paper. For review and discussion, see Bailey and DeVore (1989); Dietz et al. (1989), Bailey (1991), Perry and Dominy (2009), and Stinson et al. (2012).

Dunstan et al., 2002; Leonard et al., 2002; O'Dea, 1991;). Similar results were found among foragers in arctic and sub-arctic regions—populations who have also undergone significant dietary changes over an extended period of time, allowing for an accurate depiction of dietary trends post-transition, generations later.

Among hunters and gatherers living in arctic and sub-arctic regions, nutrition profiles differ from their counterparts occupying warmer climates closer to the equator (see Marlowe, 2007, 2010). This variation is largely based on three factors: (a) ecology, (b) access to market resources, and (c) pace of nutritional change. First, when compared to other ecological zones, cold climate foragers occupy habitats characterized as having the lowest primary biomass (Binford, 2001; Marlowe, 2005). This has extreme consequences for diet composition—with cold weather hunter-gatherers relying far more heavily on animal resources, both on land and from the sea (Kuhnlein, 1994). Rather than showing clinical signs of iron deficiency anemia, most nutrient evaluations of arctic and sub-arctic foragers suggest that they are more likely to suffer from deficiencies in vitamin A and calcium (Egeland et al., 2004; Moffatt et al., 1993; Verdier & Eaton, 1987). Second, among most populations in these regions, the traditional food base has not changed—anchored by access to varying game and marine resources, the result is that a largely traditional diet is now supplemented with processed foods and market resources (Blanchet, Dewailly, Ayotte, & Bruneau, 2000; Duhaime, Chabot, Fréchette, Robichaud, & Proulx, 2004; Kuhnlein et al., 1996; Sheikh, Egeland, Johnson-Down, & Kuhnlein, 2011). Lastly, nutrition transition among arctic and subarctic foragers has happened gradually, allowing researchers to more fully capture disease profiles among these populations. An overwhelming amount of data now suggests that rather than malnutrition, transitioning populations in these ecological zones suffer from impaired glucose tolerance, hypertension, diabetes, and obesity (Burrows, Geiss, Engelgau, & Acton, 2000; Benyshek et al., 2013; Ebbesson et al., 1998, 2005; Jørgensen et al., 2002).

Collectively, these data suggest that directly measuring micronutrient levels in blood and hair samples among foragers before and after nutrition transition show a clear trend towards increased nutritional stress post-transition. It is important to note, however, that hemoglobin status and iron deficiency anemia are multifactorial and, in addition to nutrient deficiency, are influenced by infectious chronic diseases (e.g., HIV, hemoglobinopathy, and malaria) and helminthic parasite load (Abrams et al., 2005; Huddle, Gibson, & Cullinan, 1999; Metz, 2008; Zimmermann & Hurrell, 2007). The data also suggest that, given enough time, the nutritional transition is also characterized by declines in cardiometabolic health and increases in obesity related health disorders (Benyshek, 2013).

4.3 | Oral health

The study of oral health, and specifically dental disease, is particularly important to anthropologists attempting to reconstruct diet from skeletal populations. This is largely because teeth are resistant to degradation compared to soft tissues and can, therefore, provide valuable information (Hillson, 2014; Larsen, 1995). The bioarchaeological data suggests that rates of caries and periodontal disease increased with the onset of agriculture (Ettinger, 1999; Larsen, Shavit, & Griffin, 1991). Data from living foragers, then, is critically important in evaluating oral health from populations in transition from foraging to agriculture. Only a handful of detailed studies on the oral health of contemporary foraging populations has been done.

In each of these populations, despite living in varying ecologies, evidence of a range of oral health maladies were found. No significant degree of dental crowding or **third molar occlusion** was found, yet evidence of antemortem tooth loss, caries, periodontal disease, and gross wear were all exhibited (Alaska native: Collins, 1932; Xavante of Brazil: Mayhall, 1970; Neel, Salzano, Junqueira, Keiter, & Maybury-Lewis, 1964; Lengua of Paraguay: Kieser and Preston, 1984; Australian aboriginals: Corruccini, Townsend, & Brown, 1990; Aka of the Central African Republic: Walker & Hewlett, 1990; Hadza of Tanzania: Crittenden et al., In Press).

These results lend support to the notion that foragers do not always have superior oral health when compared to agriculturalists and that the assumed decline in oral health during the Neolithic Revolution might be far more nuanced than previously thought (see Mummert et al., 2011). The mechanisms of cariogenesis are increasingly considered to be multifactorial. Caries prevalence is linked not only to the demineralization of tooth enamel and dentin by acids produced from plaque bacteria, but also to diet composition (Lukacs, 2008; Lukacs & Thompson, 2008), genetic susceptibility (Shaffer et al., 2015), the oral microbiome (Strużycka, 2014), female life history events (Lukacs & Largaespada, 2006), and concentration of salivary alpha amylase (sAA) (Scannapieco, Solomon, & Wadenya, 1994). Oral health data from foragers, those consuming a wild diet and one that increasingly includes domesticated cultigens, provide important context for renewed discussion of the links between dental disease and the evolution of the human diet.

Rather than clear-cut, the data on the health consequences of nutrition transition tell a complicated and multifaceted story where change is operating at varying paces around the world. The degree and rate of change for each population is based on ecology, social and political structures, and/or economic forces, all resulting in "nondirected change" in both the types and quantities of resources available (Kuhnlein & Receveur, 1996). Detailed studies on nutrition transition among foragers remain valuable in terms of providing insight into evolutionary models of human nutrition—as the shift from foraging to agriculture is often seen as one of the hallmarks of human evolution. In addition to direct measures of nutrition, other lines of evidence have proven to be immensely valuable in increasing our understanding of the ways in which foragers have functioned within their food system for thousands of years. One particularly fruitful burgeoning line of research is work on the gut microbiome.

5 | GUT MICROBIOME

The human microbiome is defined as the sum of symbiotic microbiota and their genomes, metabolites, and the surrounding environment (Marchesi & Ravel, 2015). The intensity of investigation on the microbiome is not unwarranted since it plays an indispensable role in the biology and evolution of all higher organisms. In this section, our goal is to demonstrate why the gut microbiome should be considered an organ that not only carries out many essential functions, but is also integral to the process of digestion and nutritional acquisition for all mammals, including humans. We also discuss how to incorporate a microbiome investigative arm alongside dietary research in anthropology, with specific emphasis on the gut microbiota.

5.1 | Microbiome as a human biological system

The human body is composed of trillions of **eukaryote** cells, but this identity is incomplete. Recent estimations suggest that the number of nucleated cells in the human body is matched 1:1 by the number of constituent microbial cells, which exert similarly vital functions, much like an organ system (Hooper, Littman, & Macpherson, 2012; Koren et al., 2012; Sender, Fuchs, & Milo, 2016; Tremaroli & Bäckhed, 2012), and the interdependent combination of these organisms is regarded as a **holobiont** (Zilber-Rosenberg & Rosenberg, 2008). Obligate symbiosis rules the domains of life (Gilbert, Sapp, & Tauber, 2012; Margulis, 1993), and humans are no exception.

The broad scope of microbial influence on human physiology, and our tenuous grasp on its underlying mechanisms, naturally invites skepticism as to its relevance in the more granular aspects of human fitness, such as reproduction and diet. However, this is easily reconciled. Epithelial surfaces throughout the body that come in contact with the environment are colonized, even before birth, by microbiota (Gilbert, 2014). As such, these microbial units serve as ambassadors of the host to the external environment. Thus, our microbial counterparts are constantly engaged in an astonishingly fluid process of molecular information exchange and feedback at the boundary between self and other. As our microbiota react to external environmental stimuli, they send signals to our own cells in a partnership that has been cultivated by evolution, giving ample reason to regard our co-resident microorganisms as “old friends” (Rook et al., 2004).

5.2 | Microbiomes for anthropology

Much of the earlier work on the human microbiome has been wholly anthropological in that it sought links between factors such as subsistence, age, sex, health, and reproduction, and the ways in which microbiome patterns vary across population demographics (De Filippo et al., 2010; Qin et al., 2012; Turnbaugh et al., 2007; Yatsunenko et al., 2012). However, by working from the other side of the equation and solving, instead, for how the microbiome impacts the human host (e.g., immune function and nutritional status), we can employ this science towards principally anthropological objectives (Benezra, Destefano, & Gordon, 2012; Gomez et al., 2016; Obregon-Tito et al., 2015; Rampelli et al., 2015). Appropriately, microbiome research also needs an anthropological perspective in order to be a relevant field of study to human biology. The cultural and environmental information derived from ethnographic research wraps a contextual world around what would otherwise be meandering explorations and incomplete data. Questions of *why* one should consider the microbiome in anthropological research can be answered simply by seeking incompletely understood observations that inundate one's foci of work, and ask whether a microbiome research component may help fill in the gaps. As for *how* to incorporate microbiome research, work typically begins with establishing what microbial taxa are present (**metataxonomics**). This should be followed with an investigation of the functional aspects of the microbiome. Functions can be inferred through gene-coding inventories (**metagenomics**), but also evaluated directly by quantifying metabolite production (**metabolomics**) or sequencing expressed RNA (**metatranscriptomics**) (Marchesi & Ravel, 2015). Anthropologists should be motivated to add a microbiome arm to their projects because this offers a body of data that can strengthen explanatory power of observations, especially considering the biologically integrative status of co-resident communities of microbiota (Amato, 2016). Since humans overwhelmingly rely on cultural modifications to navigate natural environments, microbiomes are an ideal target for evaluating the biological impacts of rapid cultural changes, even in a static environmental landscape.

Currently, only a few studies on the microbiome of human foragers and small-scale traditional societies have been done, however, several rural communities have also provided valuable evidence of the diversity of the human microbiome (see Table 1). Importantly, given the nuances in subsistence classifications that we outlined previously (see Section 2.1), relevant associations that are to be made between the microbiota and human forager diets are dependent on accurately identifying foraging of wild foods from other mixed subsistence models. While not necessarily aimed at analyzing diet composition, important information can be gleaned from the handful of microbiome studies that have been published (Burkina Faso: De Filippo et al., 2010; Hadza: Schnorr et al., 2014; BaAka: Gomez et al., 2015; Matses of Peru: Obregon-Tito et al., 2015; Yanomami: Clemente et al., 2015; Papuan highlanders: Martinez et al., 2015; Khentii: Zhang et al., 2014). An overall conclusion that we can take away from these studies is that the major observed shifts in composition and abundance are a result of the massive lifestyle changes that coincide and associate with post-industrial (and usually urbanized) societies and are not necessarily linked with evolutionary selection pressures and/or specific modes of subsistence.

5.3 | Metagenome view of diet specializations

Humans actively cultivate membership and diversity of the gut microbiome through the types of foods that they consume (David et al., 2013; Flint et al., 2008), and differences in the types and sources of nutrients in the diet, particularly lipids and plant-based carbohydrates, appear to overwhelmingly dictate the microbial taxonomic community structure (Sonnenburg & Sonnenburg, 2014; Sonnenburg et al., 2016). As diet composition influences the residency of microbial gut symbionts, so too does the microbiome play an important role in nutritional buffering for the host. Therefore, anthropologists can expect to find attributes of the microbiome that serve a nutritional-provisioning role, which has been previously studied using **batch *in-vitro*** culturing

TABLE 1 To-date list of microbiome studies conducted with traditional and rural world-wide populations

Traditional population	Region	Location	Subsistence	Food type	Data type	Body site	Study
Rural Burkinabe	Africa	Burkina Faso	Rural farming	Agricultural crops: millet, sorghum, grain flours, legumes, vegetables, herbs, occasional meat (chicken, termites)	V5–V6 16S rRNA	Fecal	De Filippo et al. (2010)
Batwa/Twa	Africa	Uganda	Formerly hunter-gatherers; horticulture, marginal foraging	Cassava, wild yams, wild game	V1–V2 16S rRNA	Saliva	Nasidze et al. (2011)
Rural Malawians	Africa	Malawi	Farming and market agriculture	Agricultural crops	V4 16S rRNA and shotgun subsample	Fecal	Yatsunenko et al. (2012)
Hadza	Africa	Tanzania	Hunting and gathering	Wild tubers, berries, baobab, honey comb, game	V4 16S rRNA	Fecal	Schnorr et al. (2014)
Hadza	Africa	Tanzania	Hunting and gathering	Wild tubers, berries, baobab, honey comb, game	Shotgun	Fecal	Rampelli et al. (2015)
Cameroon hunter-gatherers	Africa	Cameroon	Hunting and gathering	Cassava, small fauna, wild fruits	V5–V6 16S rRNA	Fecal	Morton et al. (2015)
Bantu farmers	Africa	Cameroon	Subsistence farming	Cassava, domestic meat, fish	V5–V6 16S rRNA	Fecal	Morton et al. (2015)
Bantu fishers	Africa	Cameroon	Fishing	Fish, cassava	V5–V6 16S rRNA	Fecal	Morton et al. (2015)
BaAka	Africa	Central African Republic	Mixed foraging, horticulture, and trade	Manioc root, wild yams, koko leaves, peanuts, *Irvingia* nuts, duiker	V1–V3 16S rRNA	Fecal	Gomez et al. (2016)
Bantu	Africa	Central African Republic	Farming and market agriculture	Agricultural products	V1–V3 16S rRNA	Fecal	Gomez et al. (2016)
Rural South Africans	Africa	South Africa	Rural farming and small market economy	Coarse grains, vegetables	16S rRNA pyrosequencing and qPCR	Fecal	Ou et al. (2013)
Rural Russians	Eurasia	Tatarstan, Omsk, Tyva, and Khakassia regions	Agriculture, market economy, gardens	Bread, potatoes	Shotgun	Fecal	Tyakht et al. (2013)
Khentii	Eurasia	Mongolia	Pastoralists	Fermented milk, meat	V1–V3 16S rRNA	Fecal	Zhang et al. (2014)
Tibetan herders	Eurasia	Highland Tibet	Herding	Meat and milk	V1–V3 16S rRNA	Fecal	Li et al. (2016)
Khentii	Eurasia	Mongolia	Pastoralists	Fermented milk, meat	Shotgun	Fecal	Liu et al. (2016)
Medieval monastic Germans	Europe	Medieval Dalheim, Germany	Rural farming	Wheat, cabbage, pork, lamb	V3, V5, V6 16S rRNA; shotgun; metaproteomics	Oral	Warinner et al. (2014)
Ancient Native American	North America	Rio Zape, Northern Mexico	Hunting and gathering, horticulture	Unknown	V3 16S rRNA	Fecal	Tito et al. (2012)
Hutterites	North America	USA	Rural farming	Fresh and canned produce	V4 16S rRNA	Fecal	Davenport et al. (2014)

(continues)

TABLE 1 (continues)

Traditional population	Region	Location	Subsistence	Food type	Data type	Body site	Study
Guahibo	South America	Venezuela	Rural farming	Agricultural crops	V4 16S rRNA and shotgun subsample	Fecal	Yatsunenko et al. (2012)
Guahibo	South America	Venezuela	Rural farming	Agricultural crops	V4 16S rRNA and shotgun subsample	Fecal	Obregon-Tito et al. (2015)
Matses	South America	Peru	Mixed foraging, horticulture, and paracultivation	Wild game, some wild plants, domesticated plantain	V4 16S rRNA and shotgun subsample	Fecal	Obregon-Tito et al. (2015)
Yanomami	South America	Venezuela	Mixed foraging and paracultivation	Bananas, seasonal fruits, plantain, palm hearts, cassava, land and lacustrine fauna, peccary, monkey, tapir	V4 16S rRNA	Fecal, oral, skin	Clemente et al. (2015)
Asaro and Sausi	South Pacific	Papua New Guinea	Subsistence agriculture, gardens	Taro, sweet potato, plantain, pork, fish	V5–V6 16S rRNA	Fecal	Martinez et al. (2015)

methods, but is now readily viewed through the lens of shotgun metagenomic and metabolite data. In particular, characterizing enzyme-coding genes based on a reference database (e.g. abundance or homology) is one method to profile the functional potential of a microbial community. Critically, however, gene presence does not equate to biological function, but refers to potential function; methods that capture evidence of function directly (such as culturing, **batch fermentation**, metabolite analysis, and shotgun transcriptomics) are needed to confirm the actual functionality of a particular microbiome configuration. Using a metagenomic approach, Rampelli et al. (2015) demonstrated that consumption of differentially sourced plant foods were reflected in the type and abundance of **glycoside hydrolases** found among the gut bacterial genomes of Hadza foragers of Tanzania and urban Italians. Interestingly, the Hadza gut microbiome appears to be adapted for broad-spectrum carbohydrate metabolism, and given the complex **polysaccharides** that characterize their diet, this illustrates a potential functional flexibility of gut microbiota to correspond to dietary composition. To improve and support these findings, experimental next steps might include simulating colonic fermentation using a batch-fermentation system such as a **chemostat** (Ziv, Brandt, & Gresham, 2013), or simulated *in-vitro* environments (Minekus et al., 1999). Investigative analyses in the form of targeted metabolite assays (Turroni et al., 2016) or metatranscriptome analysis (Lee, Rusch, Stewart, Mattila, & Newton, 2014) would also offer a snapshot of total activity output of the microbiome and can be used alongside dietary trials, interventions, or even recalls. These strategies may help us achieve a new level of understanding as to how, and to what extent, the human microbiome is adapted to specific dietary or environmental factors, and whether these were relevant selective forces in human evolution.

5.4 | Metabolites and nutritional buffering

The type and abundance of enzyme-coding genes necessarily impacts metabolite production, which are mostly in the form of volatile fatty acids that are the result of carbohydrate fermentation and are absorbable and used by the human host (den Besten et al., 2013). These microbiota-derived fatty acids are the key substrates that support an entire dietary class of animals, the herbivores, for whom the majority of the diet is comprised of plant cell walls. However, omnivores, particularly the great apes (including humans), are also highly dependent on microbial metabolites for nutritional support. The amount and type of carbohydrate in the diet differentially affects the abundance ratio of short chain fatty acid (SCFA) production, depending on factors such as: (a) plant and tissue type; (b) polymer resistance to host intestinal enzymes; (c) **pentose** or **hexose saccharides**, and their complexity (den Besten, 2013). A comparison between rural Africans living in South Africa with that of urban African Americans found remarkably higher total SCFA in stool of the former, with similar results reported for Burkinabe rural farmers, and was attributed to a traditional African diet rich in “coarse grains and vegetables” (De Filippo et al., 2010; Ou et al., 2013). Looking at SCFA production in terms of abundance ratio also characterizes the bacterial activity output and fermentative strategy, as in, whether the products cross-feed other microbes or whether they directly feed the host (Bergman, 1990; den Besten et al., 2013; Lambert & Fellner, 2012). Increasingly, we realize that the particular metabolic pathways that are engaged through microbial metabolite production can also induce physiological changes in the host that alter host sensitivity to incoming or derived dietary nutrients. This means that as the gut microbiota come into contact with foreign substrates (i.e., foods), they can signal to the host metabolism about the type and abundance of nutrients available, and the host metabolism can respond accordingly (Tremaroli & Bäckhed, 2012).

5.5 | Comparative work informs evolutionary hypotheses

Our understanding of the role of the gut microbiome in human diet is richly informed by comparative studies between populations with different subsistence regimes—from source, to production, to consumption (De Filippo et al., 2010; Gomez et al., 2016; Obregon-Tito et al., 2015; Schnorr et al., 2014). Furthermore, the composition and function of the gut microbiome is chiefly influenced by host gut morphology and dietary patterns (David et al., 2013; Delsuc et al., 2014; Milton & Demment, 1988; Muegge et al., 2011). A general trend has emerged in which traditional populations, regardless of geography, maintain a shared continuum of taxonomic presence and absence that does not overlap with characteristic taxa for industrial-urban populations. Therefore, mode of subsistence appears to overwhelmingly explain the presence and distribution of taxa, with hunter-gatherer groups clustering most closely together, followed by a wider spread of variation for mixed subsistence and rural farmers (Gomez et al., 2016; Martinez et al., 2015; Obregon-Tito et al., 2015; Schnorr et al., 2014).

These observations and inferences lead to more tantalizing inquiries. Can humans cultivate specific microbial communities that possess unique adaptations to metabolize novel dietary compounds, relevant to both ancient and contemporary populations? One early publication supports the idea that, indeed, horizontal gene transfer from environmental microbiota is possible and can impart beneficial dietary adaptations (Hehemann et al., 2010), though corroborative findings in other human populations are not yet available. Structural reconfigurations of microbial taxa are also well associated with short-term changes to diet (David et al., 2013), but adaptation as a result of long-term consumption or exposure to specific foods or diets is still unclear. Some evidence comes from the observation that people with **celiac disease** have a distinctly altered gut microbiome that is depleted in key phyla (Sellitto et al., 2012), although whether this is a contributor to or outcome of the disease remains unclear. In contrast, a healthy gut microbiome contains many bacterial species capable of degrading **gluten** (Caminero et al., 2014), and may be connected to an ancient dietary adaptation, or functional honing of the microbiome, following the transition to grain-based agriculture. Not only does the microbiome help degrade complex dietary molecules, but it is also critical for early training of the adaptive immune system (Hooper et al., 2012). As reports of celiac disease and **non-celiac gluten sensitivity** (NCGS) rise, both of which are often co-expressed with other autoimmune disorders, gut epithelial permeability, and **FODMAPS** (sensitivity fermentable, oligo-, di-, monosaccharides, and **polyols**) and are multifactorial in development (Biesiekierski et al., 2013; Megiorni & Pizzuti, 2012), a worthwhile investigation of gluten-degrading microorganism abundance could reveal interesting patterns of disruption, potentially as a result of environmental **xenotoxins**, such as pesticides or agricultural antibiotics (Mohan et al., 2016).

If diet alone could be associated with major changes in the genetic and taxonomic structure of the gut microbial community, and if local environments encouraged the acquisition of novel microbial traits through horizontal gene transfer with endemic microbes (Hehemann et al., 2010), then it seems likely that these processes have happened throughout human evolution. In fact, microbe-animal symbiosis is a governing principle of biology (Margulis, 1993), epitomized in examples like the bobtail squid and their luminescent *Vibrio fischeri* or coral and their photosynthetic zooxanthellae (Fraune & Bosch, 2010; Gilbert et al., 2012; McFall-Ngai et al., 2013). Examples of diet induced microbiome adaptations in animals are varied and ubiquitous, having been inferred across all mammalian phylogeny (Muegge et al., 2011), with specific observations from work on honeybees, termites, vultures, giant pandas, gorillas, and bovids (Brulc et al., 2009; Engel, Martinson, & Moran, 2012; Martinez et al., 2015; Ley et al., 2008; Muegge et al., 2011; Tamarit et al., 2015; Zhu, Wu, Dai, Zhang, & Wei, 2011). One of the most striking examples of microbiome convergence due to dietary niche is seen in **myrmecophagous** mammals (Delsuc et al., 2013).

In the few studies of traditional populations, dietary specialization of the gut microbiota are noted at the level of encoded traits, such as **strain-level** carbohydrate degrading specializations and population structuring of mobile genetic elements (Brito et al., 2016; Obregon-Tito et al., 2015; Rampelli et al., 2015; Soverini et al., 2016). Perhaps then ancient human hunter-gatherers, who lived in and subsisted upon a wild landscape, could acquire and incorporate environmental microbial traits that would confer a fitness advantage simply by providing the genetic tools to convert **refractory plant foods** into nourishing nutritional compounds. Earlier work has shown that human-associated bacteria elicit specializations following human cultural changes during the Neolithic, indicated by an expansion of transposable elements in bacterial genomes (Mira, Pushker, & Rodriguez-Valera, 2006). Therefore, it is not unreasonable to suppose that similar rapid specializations have followed humans (as well as all animals) across a multitude of ecological settings.

One intriguing possibility of a deep evolutionary source for human reliance on and rapid adaptability of the gut microbiome relates to fermented foods. Species that encounter and consume naturally fermented foods, such as primates, may gain additional exposure to specific crops of carbohydrate degrading microorganisms from the environment. Early hominid exploitation of overripe fruits is thought to have activated an alcohol metabolizing enzyme in ape ancestors and may have helped reinforce the mutualistic relationship between humans and microbiota by improving human tolerance of fermented foods and microbial metabolite byproducts (Carrigan et al., 2014), though this pattern likely extends to other primates and animals as well. Still, human directed fermentation is now a widespread behavioral trait that is used to improve the quality of a number of food resources, external to consumption, including dairy, cereal grains, and legumes. Given seasonality of resources, it appears advantageous to accommodate rapid turnovers or reorganizations of gut microbiota following food availability. The origin and effect of these behaviors is an open area of investigation, but there is potential that the extensive nutritional benefits that humans gain from fermented foods is owed to some ancient selective process.

6 | SUMMARY AND CONCLUSION

We live in a time when our industrialized modes of subsistence have never been more dissimilar to those of our past, the Neolithic farmers or Paleolithic hunter-gatherers, prompting a thrum of academic and public curiosity about the prospects of revisiting these older, more enduring, lifeways. The fact that advances in modern medicine parallel an increasing burden of chronic illness in post-industrialized western populations has not escaped public notice, and whether by fad or genuine conscientiousness, people are increasingly turning to diet and lifestyle interventions. Though the accuracy of scientific research that is distilled into the public arena certainly leaves much to be desired, there is no doubt now that the world is listening. Anthropology stands to become a potent informant of human health policy for years to come.

In this review, we have attempted to provide a bridge between anthropology, human biology, and nutrition science in order to more fully integrate data collected among foragers over the last several decades. This cross communication not only informs our understanding of cultural and ecological diversity, but also underscores the valuable contributions that a knowledge of wild diets makes to evolutionary models of dietary reconstruction.

While foraging populations have historically been used as referential models of past Paleolithic lifeways, they are increasingly being recognized as ecologically and culturally diverse contemporary populations—with their own geopolitical and social histories that define not only their interactions with other ethnic groups, but with the environment. That being said, the study of the world's foragers, in all ecological settings, offers powerful and unparalleled data that allows us to explore subsistence patterns based on wild foods in the absence of agriculture. Large compilation studies, such as those outlined in the previous sections, provide a valuable starting point to discussion—a baseline upon which we are able build a more comprehensive understanding of forager diet by including the handful of detailed, quantitative dietary studies available. Taken together, both qualitative (summative) and quantitative (population specific) data suggest that there is no one pan-forager diet, rather there is wide variation based on ecology, seasonality, and resource availability. Moving forward, as foraging populations are rapidly transitioning or have completed the transition, it is essential to acknowledge that rate of change is based not only on ecology, but is also strongly tethered to social, political, and/or economic forces. When attempting to document wild foods still consumed by foragers, it is critical to do so in a way that is both accessible to nutritionists and comparable to previous work done with less nuanced methods.

Moving forward, researchers must begin to document botanical names of foods and units of food measurement in the field, reporting raw as-eaten estimates and clearly converting them into kilocalories—the unit that appears to be the most relevant for anthropologists attempting dietary reconstructions or using such data to make behavioral inferences. If new, heretofore unpublished, analyses of botanical composition are undertaken, consideration should be paid to clearly articulate the chemical composition methods, particularly the type of method used for the analysis of fiber that captures colonic fermentation and more accurately measures all carbohydrates available to the consumer.

Our understanding and appreciation of the role of fiber in wild diets is increasing as the understanding of the evolutionary significance of the human feeding pattern is better understood. In particular, extractive foraging by an intelligent human ancestor, with a finicky habit to avoid "roughage," would remove or nullify indigestible fractions, slightly slow the rate of passage, increase small-intestinal absorption, and induce rapid colonic fermentation of foods, culminating in fairly high digestive efficiency. Additionally, traditional food processing such as cooking, pounding, winnowing, cutting, or peeling, significantly augments nutritional accessibility at all stages of digestion. Therefore, by selectively foraging for more readily digestible elements across the landscape, early hominins could avail the absorptive enhancement of the small intestine as well as increase the metabolic power of the gut microbiota, despite reductions in colon size, and ultimately achieve major gains in caloric bioavailability.

Over the past decade, the multiple "-omics" (e.g., metabolomics, metagenomics, and metataxonomics) approaches have facilitated our ability to examine microbial ecologies at an unprecedented level of detail. Although microbiome research has come under intense focus in recent years due to massively parallelized high-throughput sequencing and increasingly sophisticated computational processing, the basis for this research is not new, merely its techniques. Out of this technological revolution, microbiome research has rapidly disseminated across many different subdisciplines of human biological research, including anthropology. Microbiome studies that have worked with traditional human groups around the world are still relatively few, and are biased in number towards populations living in tropical environments such as South America, Africa, and Oceania. Their results, however, suggest that a biogeographical pattern of variation in microbiome composition is not supported. It is critical that future work characterize genome-level microbial variation in order to learn more about how the human microbiome is shaped by the environment and, therefore, may be an extra-somatic target for selective events due to lifestyle factors like diet. As more data emerge, we can build our associative and mechanistic understanding of the gut microbiome in relation to human physiology, with the end goal to project these relationships back in time where data are sparse and the macro-ecological context is unknown.

Methods of scientific inquiry are in the midst of rapid change—both in terms of technological advances and integration of a plethora of data from many disciplines. Researchers interested in reconstructing the evolution of the human diet have access to more data than ever—and this benefits those interested in pursuing diet composition and nutrition research among hunting and gathering populations. It is perhaps fortuitous, then, that the present zeitgeist is a strong public interest in evolutionary health, effectively forcing an interdisciplinary response to health research and policy. The explosion of interest in evolutionary medicine, evidenced by the current popularity of "Paleo-diets" or alternative medicine, may speak to a progressive undercurrent of realization that the factors affecting human health are immutably dictated by human evolutionary history. As a result, we have likely crossed a cognitive threshold in awareness of who we are as humans and irrevocably formalized that anthropology is the necessary partner to all endeavors in human biology, most certainly including work among foraging populations.

As the world's hunter-gatherers dwindle, these small groups are receiving a renewed time in the media and scientific spotlight—unparalleled since the 1960s and 1970s. In recognizing the active decisions that traditional populations continually make to preserve their cultural identity and autonomy, particularly in the face of substantial external pressures to acculturate, we become more cognizant that these processes likely happened in (pre)historical contexts as well, predating our formal institutional awareness of the native community landscape. Traditional populations are never in a "precontact" or "uncontacted" state. Rather, they have achieved their present-day situations out of a temporally deep gauntlet of population level interactions. Therefore, while we hope to ensure that these precious few remaining traditional groups have the dominant voice in the trajectory of their future existence, we cannot presume that any of them, no matter how isolated, have not been affected by waves of external diachronic spheres of influence. It is our sincere hope that work among foraging populations, in both cultural and biological disciplines, continues to include the voices of the people themselves as the world documents the final stages of transition for these few remaining groups.

GLOSSARY

Arabinoxylans—a polymer of the pentose sugars, arabinose and xylose, that comprises hemicellulose, found in the cell walls of plants.

Amylopectin—a polysaccharide that is one of two main components of starch (the other being amylose) which makes up approximately 70-80% of **native starch**.

Amylose—a polysaccharide that is one of two main components of starch (the other being amylopectin) which makes up approximately 20-30% of native starch.

Atwater system—a standard method of calculating the metabolizable energy (ME) content of food based on measurements of the heat of combustion of carbohydrates, proteins, and fats; it has frequently been called into question for accuracy of ME because the system does not address diet induced thermogenesis (DIT), discriminate between ileal and total tract digestibility, or account for variation in energy harvest due to the gut microbiome.

Batch fermentation—a system for fermenting a substrate using a diverse community of microorganisms under anaerobic conditions, usually in a bioreactor, until the substrate is completely exhausted and converted into metabolites; a type of batch fermentation is chemostat.

Batch in-vitro culturing—system that simulates host physiological conditions to grow and maintain viable microbial communities that function and produce metabolites as would be expected in the host organism.

Binding sites—locations on a molecule that allow an enzyme to dock and interact with that molecule.

Bioaccessibility—the portion of a substrate that is made available for absorption.

Bioavailability—originally used refer to the rate and extent that a compound reached the site of activity; has recently broadened to include the measurement of the fraction of a compound that may be absorbed into systemic circulation.

Calorie (Cal)—the commonly used parlance for a unit of food energy. See large calorie and small calorie. The term "calorie" is not officially recognized as a unit of food energy by the Committee on Nomenclature of the International Union of Nutritional Sciences.

Carbohydrates—the sugars, starches, and fibers found in foods; composed of monosaccharides (e.g. **glucose**), disaccharides (e.g. sucrose), and polysaccharides (e.g. starch and cellulose).

Celiac disease—a heritable autoimmune disorder where the ingestion of gluten can lead to severe damage of the small intestine.

Cellulose—a polysaccharide that provides the structure of plant cell walls; a source of dietary fiber that is indigestible by humans.

Chemostat—a type of batch fermentation and culturing system that enables a controlled environment in order to regulate cell growth, and allows for controlled input of fermentative substrate and removal of metabolites (products of fermentation) and cells, preventing overgrowth as well growth limiting conditions.

Cross-feed—when metabolites produced by one microbial group are used for energy by another.

Crude fiber analysis—an analytical measurement that quantifies cellulose and lignin; is no longer the standard practice for fiber analysis, as it removes other components of fiber, such as hemicellulose and **pectin**, and is there an underestimate of total fiber content.

Dicot—one of the two large groups of flowering plants or angiosperms (the other being monocot) that is defined by having a pair of leaves (called cotyledons) in the seed embryo.

Dietary breadth—the number and type of resources targeted and consumed (not to be confused with the Dietary Breadth Model used in classic Optimal Foraging Theory that ranks resources distributed across the environment in different densities according to their nutritive value and processing costs).

Dietary fiber—indigestible carbohydrates and structural components of plants.

Diet-induced thermogenesis (DIT)—Energetic cost of digestion specifically related to the generation of heat above basal metabolic rate as a result of molecular reactions involved in digesting and incorporating nutrients into tissue.

Drip loss—the loss of weight in food (typically meat) due to the dripping away of tissue juices and the evaporation of water that occurs during the process of cooking or thawing.

Dry weight—refers to the weight of a particular food with the % moisture excluded (may include inedible portion).

Enzymatic gravimetric method—analytical measurement that quantifies total, soluble, and insoluble dietary fiber in foods.

Eukaryote cells—cells with a membrane bound nucleus; also called "nucleated cells".

FODMAPS—fermentable, oligosaccharides, disaccharides, monosaccharides, and polyols typically derived from plants.

Functional fiber—nondigestible carbohydrates that have health effects for consumers.

Gelatinization—a process by which heating starch and water allows the water molecules to enter into the starch structure, causing the granules to swell.

Glucose—a carbohydrate categorized as a "simple sugar" or monosaccharide that is broken down in the body to produce energy.

Gluten—the naturally occurring proteins in found in wheat, rye, and barley.

Glycoside hydrolases—universal and ubiquitous enzymes that hydrolyze glycosidic bonds in complex glycoside sugars.

Hemicellulose—a matrix polysaccharide that is a structural component of plants that acts as an adhesive for plant walls; a source of dietary fiber that is indigestible by humans.

Hexose saccharide—a monosaccharide with six carbon atoms.

Holobiont—the host (plant or animal) plus of all its microbial symbionts.

Industrial food processing—the transformation of raw animal, vegetable, or marine resources into edible products through the application of labor, machinery, energy, and/or scientific knowledge; includes grinding, homogenization, pasteurization, defatting, liquefaction, and emulsification.

Insoluble fiber—not soluble in water.

Inulin—a polysaccharide of fructose molecules produced by plants; a source of dietary fiber that is indigestible by humans.

Joule—a form of kinetic energy that can be converted to calories and kilocalories.

Kilocalorie (kcal)—the precise term in nutrition science used to refer to a unit of food energy equivalent to 1,000 calories.

Kilojoule (kJ)—Standard unit of food energy in many countries, equates to 1000 joules.

Large Calorie—spelled with a capital "C", also known as the "kilogram calorie" or "food calorie", equates to 1000 small calories or 1 kilocalorie; technically refers to the amount of heat required at a pressure of one atmosphere to raise the temperature of 1 kilogram of water by 1 degree Celsius.

Macronutrients—nutrients that provide the most energy; include carbohydrates, protein, and fat.

Metabolite—the products of metabolism.

Metabolomics—the quantification of the profile of metabolites produced by a community of organisms or tissues.

Metagenomics—the study of all genes and genomes in a given sample.

Metataxonomics—the study of the taxonomic profile and relationships of organisms in a given sample.

Metatranscriptomics—the study of all expressed RNA in a given sample by sequencing the complimentary DNA (cDNA).

Methanogens—archaea that produce methane as a byproduct of metabolism.

Microbiome—the sum of symbiotic (i.e. co-residing) microbiota and their genomes, metabolites, and the surrounding environment.

Microbiota—viruses, bacteria, archaea, and single and multicellular eukaryotes.

Micronutrients—nutrients that include vitamins and minerals.

Mismatch hypothesis—the idea that organisms, including humans, are adapted to a past evolutionary environment and possess traits that conferred a selective advantage in that ecology which are currently "mismatched" to the current environment; also referred to as "evolutionary discordance".

Moisture content—the amount of water in a food, often expressed as a percent; typically calculated as the difference in sample weight of food from fresh to dry and then divided by the original fresh weight of the food and multiplied by 100.

Monocot—one of the two large groups of flowering plants or angiosperms (the other being dicot) that is defined by having only one leaf (called a cotyledon) in the seed embryo.

Monosaccharide—the most basic unit of a carbohydrate; also called "simple sugar"; an example of a monosaccharide is glucose.

Monounsaturated fatty acids (MUFAs)—a type of fatty acids; defined chemically as having one double bond in the fatty acid chain with all other carbon atoms single bonded.

Native starch—starch granules derived directly from the plant source without altering their chemical structure (i.e. undamaged and ungelatinized).

Myrmecophagous—a feeding behavior characterized by the consumption of termites and/or ants.

Neutral-detergent fiber—structural polysaccharides that are dissolved using a neutral detergent in chemical composition analysis and have low digestibility.

Neutral-detergent fiber analysis—an analytical measurement that quantifies some of the indigestible components of plant foods, such as lignin, cellulose and hemicellulose, but does not measure pectin.

Non-celiac gluten sensitivity—a condition where people consuming gluten exhibit symptoms that are similar to those seen in celiac disease, yet lack same antibodies and intestinal damage seen with celiac disease; also known as "gluten sensitivity".

Oligosaccharide—a carbohydrate composed of 2 – 10 simple sugars linked together; must be broken down to smaller units for absorption in humans.

Pectin—a family of complex polysaccharides found in the primary walls of plants; a source of dietary fiber that is indigestible by humans.

Pentose saccharide—a monosaccharide with five carbon atoms.

Polyols—sugar alcohols.

Polysaccharide—long chains of monosaccharides or disaccharides that are synthesized by plants and animals (including humans) to be used or stored for structure or energy; storage polysaccharides include starch or glycogen, and structural polysaccharides include cellulose.

Polyunsaturated fatty acids (PUFAs)—a type of fatty acids that includes the essential fatty acids (Omega-3 and Omega-6 fatty acids) among other fatty acids (like conjugated fatty acids); defined chemically as having two or more double bonds in the fatty acid chain.

Prebiotic—non-digestible substances that act as food for gut microbiota.

Probiotic—an exogenous microbial supplement.

Refractory plant foods—Foods in which the energetic nutrition is locked away in resistant forms such as cellulose, hemicellulose, inulin, pectin, and native starch.

Resistant starch—>starch that resists enzymatic degradation, typically all native starch exposed to human alpha and beta amylases.

Short chain fatty acids (SCFAs)—a type of fatty acid that are produced when resistant starches and dietary fiber are fermented in the colon.

Small calorie—spelled with a lowercase "c", also known as the "gram calorie" or the "15° calorie"; technically refers to the amount of heat required at a pressure of one atmosphere to raise the temperature of 1 gram of water 1 degree Celsius. It equates to approximately 4.2 joules.

Strain level—characterization of subgroups microorganisms that otherwise share genetic homology at the level of species (98.9% based on the 16S rRNA gene), based on the variance of specific genes across genomes.

Soluble fiber—soluble in water.

Starch—source of carbohydrate that can be divided into two components, amylose and amylopectin; digestible by humans.

Sugar—general term for soluble carbohydrates.

Third molar occlusion—when the upper and lower molars are in functional contact.

Traditional food processing—the purposeful external modification of a resource to change its physical or chemical attributes in preparation for consumption; uses non-mechanized technological methods of food processing, such as: fermentation, germination, mechanical processing, thermal treatment, dehydration, and preservation.

Wet weight—the fresh raw weight of a food with percent (%) moisture included (may include inedible portion).

Xenotoxin—a toxin originating outside of the body; examples include pesticides or antibiotics.

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