

Who Is a Hunter-Gatherer?

Anthropological Concepts and Their Use in Microbiome Research

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Abstract *In this chapter, I critically assess the use of the category of hunter-gatherers in human microbiome research. Reviewing debates on the category within the interdisciplinary field of hunter-gatherer studies, I reconstruct the resulting complex and critical stances of archaeologists and anthropologists. I show how these often get lost when microbiome researchers assume this category. I use these insights to complement a growing literature on race and related categories in human microbiome research. This literature emphasizes political and ethical issues concerning racism and representational violence, as well as exploitation and bioprospecting. I argue that awareness of debates in hunter-gatherer studies can add more depth and nuance to this critical assessment. Additionally, I show how these debates can improve microbiome research on hunter-gatherers, as they highlight important methodological and epistemological problems concerning generalization and analogical reasoning.*

Introduction

The use of race or related categories in various fields involved with genomic concepts and technologies, from human evolutionary biology to biomedicine to forensics, has been analyzed and criticized by many authors in the humanities and social sciences since the formation of the Human Genome Project.¹ A relatively recent field of research that is enabled by genomic technologies is microbiome research. This chapter addresses human microbiome research and asks how naming populations plays out in this field. One way of naming populations that gained prominence in microbiome research is based on typologies of modes of subsistence (Ellen 1994), which were developed and are used in archaeology and various subdisciplines of anthropology, and consist of categories such as hunter-gatherer, pastoralist, agriculturalist, etc. This transfer of concepts can be problematic when important insights from the context of origin get lost. Here I investigate

1 For the relevant literature, see references in the introduction to this volume. The history of race in biology and medicine and its criticism goes back much further; see, e.g., Ernst and Harris (1999).

to what extent this is the case and what the consequences are for research on hunter-gatherer microbiomes.

Adding to the literature on race in biomedicine and other genomics-driven fields, there is a small, but growing literature from the humanities and social sciences that scrutinizes how race and related categories figure in human microbiome research (Benezra 2020; Chellappoo and Baedke 2023; De Wolfe et al. 2021; Helmreich 2016, Ch. 6; Hobart and Maroney 2019; Hutchison and Núñez Casal 2023; Nieves Delgado and Baedke 2021; Raffaetà 2022; Rawson 2024; Rowland 2020). Some authors thematize microbiome studies on populations with perceived traditional ways of life, including hunter-gatherers, but often discuss them in combination with other studies that compare microbiomes of populations within industrialized societies that are identified in terms of race or ethnicity. The conceptualizations of modes of subsistence and race or related categories are doubtless historically and practically intertwined. It thus makes sense for scholars with a focus on race to cover a continuum of cases where race categories, processes of reification of race, and the reproduction of racial stereotypes and racialized injustice play out. Nonetheless, race and subsistence modes are quite distinct ways to categorize people, and each follows a different logic. Subsistence types are decidedly seen as not pertaining exclusively to groups identified by geography or ancestry. The scheme runs orthogonal to race classification. Hence, while the above-mentioned commentators put the focus on race, where the categorization of populations as hunter-gatherers is but one among other problematic aspects, I complement this work by focusing on the category of hunter-gatherer directly, where its role in racialized discourse is but one problem, among others.

The category of hunter-gatherers or foragers is usually part of a classification of different modes of subsistence, including fishers, pastoralists, or herders, horticulturalists, agriculturalists, and other categories (Ellen 1994). The number of categories recognized, as well as their names and meanings, differ between authors, fields, or traditions, and change over time. However, the category of hunter-gatherer takes a special position. Paleoanthropologists believe that archaic hominins, at least from *homo erectus* evolving almost two million years ago, lived as hunter-gatherers (Robinson 2014). And so did modern humans, *homo sapiens*, which emerged about 300,000 years ago, until ca. 12,000 years ago, when the domestication of plants and animals set in (Ellen 1994). Hence, other modes of subsistence only emerged after the evolution of hunter-gatherer ways of life, and only recently in evolutionary time-scales. For this reason, from science to pop-culture, modern humans are seen as having evolved as hunter-gatherers (Lavi et al. 2024). This fact lends special significance to this category as opposed to other modes of subsistence and is one reason why otherwise methodologically and conceptually very diverse disciplines came together in a field called “hunter-gatherer studies.” It also explains the expansive interest in contemporary populations that are identified as hunter-gatherers, despite the small numbers. Knowledge about these populations is often considered to be informative about prehistoric humans. This is also one of the motivations for microbiome researchers to study these populations, in addition to an interest in synchronic, epidemiological differences between populations.

My analysis is based on three separate bodies of literature. I will first reconstruct some debates on the category of hunter-gatherers within hunter-gatherer studies and the resulting complex and critical stances towards the category in the field. Next, I will

show how this complexity initially is lost when microbiome researchers use the concept to classify populations from which they collect samples. I will then draw on the critical science studies literature, mentioned above, to highlight the political and ethical consequences of this neglect. I aim to show how learning from the debates in hunter-gatherer studies can add to the critical assessment of research on hunter-gatherer microbiomes. I use the insights from my analysis to articulate further epistemological criticism of using the hunter-gatherer category in an unqualified manner. Eventually, these considerations could help to improve scientific practice (Benezra et al. 2012).

Hunter-Gatherer Studies and Its Debates

Based on travel reports, populations that were later referred to as foragers or hunter-gatherers have been part of European scholarly discourse at least since the sixteenth century.² They were subject to empirical fieldwork in archaeology and anthropology since the second half of the nineteenth century. Here, I will focus on the debates that unfolded after the 1960s and shaped the contemporary understanding of the category. The 1966 conference “Man the Hunter” and the subsequent publication of a volume by the same title (Lee and DeVore 1968) are usually perceived as crucial events in the emergence of hunter-gatherer studies as an interdisciplinary field, bringing together anthropology, archaeology, and other disciplines (Jordan and Cummings 2014). The field consolidated through the Conferences on Hunting-and-Gathering Societies (since 1978), the journal *Hunter-Gatherer Research* (since 2002), the *International Society for Hunter-Gatherer Research* (since 2014), and numerous collected volumes and handbooks.³

While the category of hunter-gatherer has functioned productively in catalyzing interdisciplinary exchange, it thereby became subject to critical debate. Initial work in the field was strongly influenced by cultural ecology originating in the United States and associated with Julian Steward (1902–1972). This was a materialist, natural science–oriented approach in which aspects of culture and social organization were analyzed as adaptations to environmental circumstances (Barnard 2014; Jordan and Cummings 2014). The view encouraged empirical approaches, but the focus was on those aspects that could be measured and related to environmental factors, such as energy expenditure, division of labor, or demography (Guenther 2007). Hunter-gatherer studies was thus a field in which cultural anthropology interacted with biological anthropology, the study of biological variation in relation to geography and environment. Furthermore, the goal to formulate generalizable socioeconomic, cultural, or ecological patterns that apply, albeit with local variations or exceptions, to many hunter-gatherer societies, strongly supported archaeologists’ strategy of analogical inference from contemporary to ancient populations. Not only did anthropology inform archaeology, but archaeologists began to conduct fieldwork themselves, a program referred to as “ethnoarchaeology” (Lane 2014).

The editors of *Man the Hunter*, Irvén DeVore (1934–2014) and Richard B. Lee (*1937), attempted to provide a paradigmatic characterization of hunter-gatherer societies, past

2 For histories of the idea of hunter-gatherers, see Barnard (2014) and Pluciennik (2001).

3 <https://www.ishgr.org/>, last accessed 11 October 2024.

and present, referred to as the “nomadic style” or later “foraging mode of production” (Lee and DeVore 1968, 11–12; see Guenther 2007; Jordan and Cummings 2014). On this view, the key social and economic features were that hunter-gatherers live in small groups, or “bands,” which are, however, linguistically and reproductively interconnected; that they move in larger geographical areas, but have a camp as their home base; and that males hunt, while females gather, where in general all food acquired is shared among the community. From this, the authors derived further implications regarding behavioral patterns, including an egalitarian social order with little personal property, a dynamic exchange between groups and reformation of groups with a tendency to keep group size low and for strategies to avoid conflict, as well as immediate food production with little storing of surpluses. While the conference participants did not agree on a definition and while the above characterization was not as consensual as it was presented, it provided a baseline against which research questions could be formulated and nonconforming patterns of behavior could be described, thus helping the interdisciplinary research program of hunter-gatherer studies to coalesce around a shared set of questions and themes. For instance, feminist anthropologists such as Sally Slocum (*1939) questioned the neglect of the contribution of woman to subsistence and social organization (Sterling 2014).

Lee and DeVore had been codirecting the Harvard Kalahari Project since 1963, which focused on the !Kung San.⁴ This population thus served as the exemplar in the formulation of the paradigm. However, anthropologists working in other geographical areas, as well as archaeologists, found it difficult to align their findings with the paradigmatic model. Environments vary substantially across geographical regions inhabited by foragers. For instance, in the presence of waters, populations will engage in fishing and according to what is available, some populations predominantly hunt, while others predominantly gather. Accordingly, the diets of some populations involve large amounts of meat, while others are mainly plant-based (Ellen 1994). Differences in environments and diets could also be observed or assumed for ancient populations. For early hominins, the degree of hunting and the role of scavenging is still discussed (Robinson 2014). Additionally, some groups might exhibit more sedentary behavior, larger groups, or more complex organization. Such variation was observed for contemporary as much as for ancient hunter-gatherers (Guenther 2007). Accordingly, some authors suggested distinctions, such as simple vs. complex or immediate vs. delayed return hunter-gatherers. However, even these came to be criticized “for reducing the inherent flexibility and variability of forager behavior, social structure, and ideology into rather simplistic oppositional categories” (Jordan and Cummings 2014, 11). As early as the 1970s, researchers also became more attuned to the increasing external threats to hunter-gatherer societies and the resulting changes. Furthermore, while there were already anthropologists interested in the symbolic or religious aspects of hunter-gatherer societies involved in *Man the Hunter*, most famously Claude Lévi-Strauss (1908–2009), to whom the volume was dedicated, towards the end of the twentieth century, there was a marked move “beyond ecology” (Guenther 2007, 378). This not only added to the sense of diversity of hunter-gatherer

4 While they initially used “!Kung Bushmen,” !Kung San and Ju/’hoansi, became the most commonly used designations in the literature. Nevertheless, the dynamics of foreign and self-designation of groups and subgroups remain contested.

lifeways, but also indicated that not all aspects, even of the hunting and gathering activities themselves, could be explained in ecological-adaptive terms.

While the nomadic-style paradigm served as a foil to describe diversity, diversity undermined generalizations in the field. In the light of observed variation, it appeared increasingly difficult to identify characteristics that hold for hunter-gatherers *as such*. Some suggested negative definitions: “It is the absence of elaborate mechanisms for regulating the environment which is perhaps the most significant characteristic of a food-collecting way of life” (Ellen 1994, 202). However, it has been suggested that hunter-gatherers manage their resources and through their activities strongly shape the environments which they inhabit (Fowler and Turner 1999). Others then take an even more relativistic stance and define hunter-gatherers as “people whom anthropology has traditionally recognized as hunter-gatherers” (Kelly 2013, 2). Variability then becomes central as that which is to be explained. Patterns of similarity and difference need to be explained with respect to similarities and differences in environments or contact with other populations or agents.

Accordingly, regarding modes of subsistence, there is little coherence in the classification of (sub)types. The literature on typological reasoning in science suggests that typologies are often implicit, their usefulness and methodological soundness is context dependent, and they usually remain subject to revisions (Love 2009). When dealing with biological or social entities, variability is not simply a question of noise in the data that can be filtered out by the appropriate statistical or rhetorical means; instead, it is constitutive of the very domain of phenomena. Nonetheless, the history of biological and social sciences shows that typologies, which turn out to be useful in some contexts, tend to become interpreted in an essentialist manner (Dupré 1993). Their categories are taken to name natural kinds, i.e., a class of things characterized by defining properties and stable across contexts and time.

From the late 1980s onwards, the initial essentializing and universalist assumptions of the field of hunter-gatherer studies came under intense criticism, from external commentators, e.g., in feminist science studies (Haraway 1989), as well as from within the field. In a controversy that came to be known as the “Kalahari debate” or “Revisionist debate,” some archaeologists and anthropologists termed “revisionists” described others as “traditionalists” or “isolationists.” Traditionalists were accused of treating living hunter-gatherers as representing a type that resulted from human evolution and that was maintained intact as an archaic, but in itself ahistoric entity, isolated from the history of changes that came with agriculture, colonialism, and industrialization. This idea of the primitive and pristine “Bushmen,” revisionists argued, was a fiction about the Other of civilization that was created in reaction to anxieties of modernity felt in Europe and North America, especially in light of the threat of nuclear annihilation and a sense of disenchantment (Wilmsen 1989; Wilmsen et al. 2009). Thus, the concept of hunter-gatherers was seen as a result of the specific Cold War and counterculture sensitivities of the 1960s, the period when the field of hunter-gatherer studies took shape (Guenther 2007). Revisionists, instead, pointed to a long history of contact between hunter-gatherers and their pastoralist or agriculturalist neighbors, as well as the more recent history of colonial encounters and interaction with state agencies and NGOs. They gathered evidence that living and past hunter-gatherers typically were engaged in trade, worked for herders and

farmers, and even pursued limited horticulture and herding themselves. Many traits of these populations, including some features described as archetypical by traditionalists, were described as the result of diverse and specific histories of interactions (Headland and Reid 1989). Some described hunter-gatherers as “a kind of impoverished rural underclass, which had been pushed into marginal areas through the impacts of wider economic and political developments” (Jordan and Cumming 2014, 14; see Wilmsen 1989). The position has been rejected as postmodern cynicism and the oversimplified framing of traditionalists’ views, as well as the evidence for and notion of “rural proletarians” have been criticized (Lee 1992, 42). Nonetheless, the debate focused on the concerns with the central category of hunter-gatherer studies and its essentialist understanding. Most in hunter-gatherer studies today accept the importance of histories of interactions (Canon 2014).

In response to these debates, a quarter of a century after the publication of *Man the Hunter*, one of the editors diagnosed a “crisis in hunter-gatherer studies” and concluded: “Even if it is agreed that hunters and gatherers exist, almost everything else about them is a matter for contestation” (Lee, 1992, 31). The reframing of hunter-gatherers as having a history “called into question the very empirical and epistemological basis of modern hunter-gatherer studies” (Jordan and Cummings 2014, 14). As Jordan and Cummings observe, “[p]articularly problematic was the implicit choice within hunter-gatherer studies to portray modern forager groups as relatively pristine, isolated, and self-sufficient units, whose internal dynamics were stripped of both history, as well as the effects of participating in wider spheres of interaction” (ibid.). Especially the analogy between living populations described as hunter-gatherers and Paleolithic populations, or what has been termed the “living fossil trope” (Guenther 2007, 373), was questioned by observations of ecological and cultural diversity and the histories of interactions and change. Hence, neither could living hunter-gatherers be seen as pristine representatives of an original humanity, nor could findings about extant groups be straightforwardly extrapolated to ancient populations. The question of which and how inferences can still be made from contemporary to prehistoric populations, then, is highly contested (Lane 2014; Marlowe 2005).

Many in hunter-gatherer studies continue to work in a narrow behavioral-ecology framework. Some still find a generalizing characterization on hunter-gatherers useful (Winterhalder 2001), while others acknowledge diversity (Kelly 2013). In any case, most researchers in the field are aware of the expanding insights on the historical and contemporary interactions and the cultural complexity, as well as the critical debates on previously unquestioned assumptions, and at least take them into account as important caveats when interpreting their data. Many work towards research agendas that forego generalization attempts and synthesize ecological and historical views, or focus on local, historically contingent social, economic, and political situations of what has been termed “postforaging societies,” e.g., regarding the effects of tourism (Guenther 2007, 382). Additionally, ethnographic research is increasingly seen as conducted for and with members of the (post-)hunter-gatherer communities, partly as active investigators, partly in the context of their political activism (Guenther 2007). Hunter-gatherer studies (as cultural and physical anthropology and archaeology in general) came to reflect on its colonial

past, the exploitative aspects of its research, and its postcolonial positioning, especially also in the context of apartheid South Africa (Barnard 2007; Schramm 2016).

In the following, I will turn to research on the microbiomes of hunter-gatherers and assess this work in the light of these developments and debates in hunter-gatherer studies.

Hunter-Gatherers in Human Microbiome Research

Research on the Hunter-Gatherer Microbiome

The interest, from a medical perspective, in hunter-gatherer lifeways is not new. In Darwinian medicine, researchers speak of an environment of evolutionary adaptedness or EEA (see Méthot 2015). It is often said that the species *homo sapiens* was characterized by a hunter-gatherer way of life for 99 percent of its existence.⁵ Hence, the argument goes, the environment encountered by Paleolithic hunter-gatherers constitutes the environment to which modern humans are adapted. On this view, due to changes in lifeways, in particular the emergence of agriculture, urbanization, and industrialization, the environments in which most humans live today are quite different from the EEA. Under the assumption that genetic evolution happens at a slower pace than these changes, a mismatch between human physiology and the conditions under which most people live can occur. While some aspects of this maladaptedness have been mitigated by technology, it is nonetheless seen as having various health consequences. In particular, low-fiber, high-fat diet and sedentary lifestyle have been recognized as leading to health problems, such as type 2 diabetes or cardiovascular diseases, prevalent in industrialized societies. In this context, hunter-gatherers are seen as a baseline or model for estimating the divergence of populations, especially Western ones, from the diet and behavior to which humans are thought to be adapted and the related physiological processes, e.g., regarding energy expenditure (Pontzer et al. 2018).

Likewise, research on the human microbiome is interested in the evolutionary dimension of the ecological relation of human hosts and their microbiota.⁶ Microorganisms not only fulfill specific metabolic functions, such as fiber degradation, but are also thought to influence and regulate the immune system, especially during development. The hygiene revolution, beginning in the nineteenth century, came to be seen as not only protecting humans from dangerous infectious diseases, but also as limiting the exposure to infections in general and to specific microorganisms that were part of the EEA

5 This phrase, often cited in microbiome and Darwinian medicine research, goes back to the volume *Man the Hunter* (Lee and DeVore 1968, 3). For a critique of this number, see Lavi et al. (2024, n33).

6 The sum of microbes present in an ecological setting of interest, e.g., the human gut, is typically referred to as “microbiota.” The term “metagenome” is used to designate the sum of the genomic material collectively harbored by the microbiota (sometimes together with the host). “Microbiome” is used to refer to the microbiota as communities and as represented through their metagenome, i.e., as studied through genomics and other “omics” technologies (Berg et al. 2020). While these terms can include archaea, protists, fungi, and viruses inhabiting the ecosystem in question, they are often used to refer only to bacteria.

of humans. The hygiene hypothesis and the old friends hypothesis suggest that this lack of exposure resulted in allergies and other chronic inflammatory and autoimmune diseases (Lorimer 2020; Raffaetà 2022). Next to their role in the development of the immune system, the microbiota of various organs have been implicated in other noninfectious diseases, from cancer to neurological disorders. Here, the idea is that, unlike in the case of infectious disease, where it is typically a single species whose presence is seen to cause the disease, the involvement of microbiota stems from some kind of disbalance or community-level metabolic processes in the host-microbe ecosystem (dysbiosis).

The Human Microbiome Project (HMP), funded initially from 2007 to 2014 by the U.S. National Institutes of Health (NIH), focused on mapping microbiomes at various sites of the human body and estimating the diversity of microbial communities across healthy individuals, including comparisons across populations identified by conventional categories of race or ethnicity. It aimed to establish a framework for the association of microbiome composition and diseases. A second phase, the integrated HMP (iHMP), emphasized pregnancy and birth, as well as specific diseases (esp. inflammatory bowel disease and type 2 diabetes), and aimed at a functional analysis of the microbiome (The iHMP Research Network Consortium 2014). These high-profile projects were mainly focused on Western populations, with much of the work being conducted in the US context. However, humans acquire their microbiome from the environment, and it is modulated by the food they eat, physical activity, and medication. Hence, microbiome researchers became interested in comparing the microbiomes of populations who live in different environments, subsist on different food sources, and differ regarding their access to health care systems. The key distinctions in this respect are typically framed in terms of urban vs. rural environments and industrialized/developed vs. nonindustrialized/developing countries, where the latter distinction is often made with reference to the Human Development Index (HDI, e.g., Groussin et al. 2021).

Since the early 2010s, several, now well-cited studies have appeared that compare populations globally (De Filippo et al. 2010; Yatsunenکو et al. 2012). These researchers mainly had backgrounds in biomedicine and genomics (partly with links to the HMP), were interested in the role of the microbiome in health and disease, and framed their work in evolutionary terms. Investigating the effects of “Westernization,” researchers collected samples from children (and adults) from rural communities in Africa and South America, respectively, and compared them with populations in Europe or the United States (Yatsunenکو et al. 2012, 222).⁷ In a similar vein, researchers turned to populations identified as hunter-gatherers. Clemente et al. (2015) collected samples from various body sites of members of a Yanomami Amerindian village, which the researchers described as “uncontacted.”⁸ The main outcome of these studies was to demonstrate a marked difference in the microbial diversity between non-Western, rural populations, and those exhibiting a Westernized lifestyle. Additionally, differences in microbiome composition between populations were observed. These studies supported the notion that environmental exposure and especially diet, as well as hygiene practices,

7 For a critical, ethnographic science studies perspective on the work behind Yatsunenکو et al. (2012), see Benezra (2020).

8 For a science studies perspective on this work, see Hutchison and Núñez Casal (2023).

frequency of cesarean birth, and antibiotics use, shape the human microbiome and that the loss of microbial diversity in Western populations might indeed be associated with the prevalence of certain noninfectious diseases.

At the same time, biological and evolutionary anthropologists and archaeo- and paleobiologists began to apply microbiome research in studies on hunter-gatherers (e.g., Nasidze et al. 2011). The Hadza, or Hadzabe people in Tanzania, similarly to the !Kung San, have been studied extensively by anthropologists with a great variety of questions and methods. Both groups are often treated as paradigmatic exemplars or models for hunter-gatherers. One expert on the Hadza, Frank Marlowe, can be considered a post-revisionist debate anthropologist who rejects the notion of a “living fossil” and takes the effects of a history of interactions into account, while nevertheless insisting that, with caution, contemporary hunter-gatherers can be treated as “the most relevant analogs for at least Late Pleistocene humans” to test hypotheses on human evolution (Marlowe 2005, 65). A collaborative project led by a yet younger generation of evolutionary anthropologists (Alyssa Crittenden) and paleobiologists (Amanda Henry), but also involving Marlowe, studied the gut microbiome of the Hadza. In contrast to the studies discussed above, the emphasis was on understanding human evolution, with the medical significance presented only as a secondary benefit. In one of their articles, they emphasize that the Hadza are genetically modern humans, but suggest that it is “likely the Hadza persist with a very ancient traditional lifestyle into present times” and that the Hadza gut microbiome diversity “is almost certainly the ancestral state for humans” (Schnorr et al. 2014, 9–10). In a more public-facing *Nature* piece, the lead author, Stephanie Schnorr, associates the Hadza with the “wild” and writes: “Thanks to the Hadza, we know that ancient human hunter-gatherers must have maintained a direct and persistent interface with the natural environment” (Schnorr 2015, S15). Due to their location in Eastern Africa, the Hadza are represented as inhabiting the same geographical space, and by implication the same environment, as early humans (i.e., the EEA).

Just a couple of years later, a group led by Justin Sonnenburg (who has a background in biochemistry and biomedicine), along with collaborators (some of whom were involved in the HMP and the Yanomami study), also turned to the Hadza (Fragiadakis et al. 2019; Smits et al. 2017). Though citing Marlowe, this group was less connected to hunter-gatherer studies. Their agenda focused on the gut microbiome in health and disease, but they still describe the Hadza as offering insights into the coevolution of humans and their microbiota. The strategy here, again, rests on comparing industrialized and nonindustrialized populations, with an emphasis on biomedical benefit for Western societies. The Hadza are characterized as “unperturbed” (Fragiadakis et al. 2019, 216), and while the populations in question are described as “just as genetically modern as industrialized populations,” their lifestyle is referred to as “traditional” and it is assumed that “in the absence of forces associated with urbanization, it is likely that these populations harbour microbiotas that are more similar to ancestral microbiotas” (Sonnenburg and Sonnenburg 2019, 385).

This brief overview of current research serves to illustrate how the microbiome of hunter-gatherers became established as a research topic, albeit pursued by researchers with different backgrounds and goals (evolutionary anthropology vs. biomedicine). This research is often presented with a sense of urgency, based on the observations that

hunter-gatherer ways of living are quickly fading out as the populations identified in these terms face various pressures to change their behaviors (Gibbons 2018). In the following, I will discuss some problematic issues in the context of this kind of research.

Hunter-Gatherer Microbiome Research and Its Discontents

Certainly, much can be learned from a comparative approach to human microbiomes, including the study of populations living in ways that are relatively unaffected by industrialization. Nonetheless, given the problematic status of the category of hunter-gatherers, the aims of some of the researchers, the assumptions they make, and the conclusions they draw, it is fair to say that the growing number of studies on the microbiomes of hunter-gatherers require further scrutiny to guarantee sound, useful, and equitable science. The critical science studies literature on microbiome research has emphasized political and ethical dimensions in terms of racism and exploitation; I will discuss these and add epistemological aspects of problematic generalizations and inference.

Referencing the microbiome studies mentioned above, science studies scholars have pointed out how microbiome research on Indigenous populations, and especially on hunter-gatherers, can “reify racist views of difference” (Rawson 2024, 5) or constitute a “reviving of colonial science” (Maroney 2017). Describing populations as “ancient” or “ancestral” (in some aspects at least), representing them as “uncontacted” or “isolated” and as living in the “wild” or closer to (an original state of) “nature,” or discussing them in comparison to early hominins or even primates, places them on a linear trajectory from “primitive” (the meaning shifting between primary, basic or fundamental, and simple) to “civilized” that can be interpreted in evolutionary or valuative terms.⁹ Despite the rejection of notions like “living fossils” or “missing links,” this trajectory is reminiscent of colonialist social evolutionism. Furthermore, this language might be perceived as offensive or as a form of violence by populations involved in a study (Mangola et al. 2022). Even where the state of a population marked as “ancient” is valued higher than the “civilized” state in terms of health, this echoes the trope of a “noble savage” (Rawson 2024). Such framings are especially problematic when they occur in popular science, as exemplified by the activities of the publisher and entrepreneur Jeff Leach, who also participated in the studies by the Sonnenburg group (see Hobart and Maroney 2019; Lavi et al. 2024; Rowland 2020). When populations are described in biological terms, this can often amount to a naturalization of social or cultural differences. Associating populations identified as hunter-gatherers with characteristic microbiomes can lead to renewed essentialist understanding of hunter-gatherers, now as a biological category.¹⁰

The often implicit and sometimes explicit primordialism is thus in itself problematic. But it also has consequences. De Wolfe et al. (2021) aim to identify “ghost variables,” which they define as “complex, historically loaded racial categories used in microbiome research without explicitly naming race” (ibid., 1; see also Benezra 2020). Ghost variables

9 For analysis of these notions and their effects, see the literature cited in the introduction, for a review, see Rawson (2024).

10 See Nieves Delgado and Baedke (2021) for a related discussion regarding microbiome research and race.

serve to evade the discussion of racism or racialized injustice especially regarding health disparities. The authors describe “hunter-gatherer” as ghost variable, although I would argue that the category functions in this way only where it is associated with attributes such as “pure,” “pristine,” “ancient,” “traditional,” etc., as opposed to “Western,” “industrialized,” etc. In the studies on the Yanomami or the Hadza, even though these populations are represented as healthy with regard to their microbiome, their framing as inhabiting an archaic environment can render invisible the effects of the interaction with neighboring groups, tourists, and state agents or NGO workers, including physicians, in postcolonial contexts and the impact of resulting potential health threats such as stress, pollution, or infectious disease. Especially, in post-settler colonial contexts, where Indigenous groups, including postforager groups, are often studied because certain health problems are especially prevalent in these populations, the structural reasons for health inequality can be masked through ghost variables. Hence De Wolfe et al. suggest making explicit the associated factors (e.g., dietary differences, pollution, variation in family structures etc.) and structural drivers (capitalism, colonialism, segregation, etc.) linked to microbiome change, instead of using ghost variables. Done right, they argue, microbiome research can also help alleviate racism and health injustice.

Rendering populations as “premodern,” “pristine,” or “ancient” with regard to certain biological aspects such as their microbiomes (even when emphasizing genomic modernity) presents them as somehow less human compared to Western populations and thus “obscure[s] Indigenous People’s agency and rationalizes the instrumentalisation of their microbial diversity for the benefit of privileged segments of neoliberal societies” (Hutchison and Núñez Casal 2023, 21). Microbiome research can thus reproduce a colonial logic in which representational violence and exploitation are two sides of the same coin (Benezra 2020; Hutchison and Núñez Casal 2023; Maroney 2017; Rawson 2024). This then highlights another ethical and political point, concerning the risk that microbiome research on Indigenous populations will facilitate bioprospecting and exploitation. Especially studies like those of the Sonnenberg group aim at eventually improving the health of Western, mainly White populations, where diseases that are potentially related to the reduction of microbiome diversity are prevalent. This research is also connected to attempts to build biobanks that store samples from populations exhibiting lifeways that are expected to disappear.¹¹ This scenario is prone to reproduce a logic of (post)colonial extractivism, in which sampled populations in the Global South are treated as natural resources, whereas benefits fall to companies and affluent sections in Western countries.

Some microbiome researchers are aware of these problems. In a conversation with (and cited by) the social anthropologist Matthäus Rest that probably expresses an ethical concern as much as a sense of competition, Schnorr deplors researchers “who search for the golden shit to correct the Western diet and want to capitalize on it” (Rest 2021, S358). Crittenden describes how interaction with her Hadza informants made her change her practices (Crittenden 2020). Schnorr and Crittenden, together with a member of the Hadza and an Indigenous anthropologist, have coauthored a paper that works towards ethical principles for microbiome research with Indigenous communities (Mangola et al.

11 Benezra speaks of “salvage microbiomics” (2020, 7).

2022). They address questions of informed consent, as well as compensation and benefit sharing. And while Schnorr and Crittenden have used such terminology before, they now recommend avoiding terms such as “traditional,” “ancestral,” “wild/re-wild,” “non-modern,” “uncontacted,” or “non-industrial,” as their use “is based on concepts of linear evolution: the idea that there is a linear gradient of human subsistence activity” and can reproduce racist ideas or be experienced as offensive (Mangola et al. 2022, 752). However, researchers might ignore such principles, and as research is often carried out by international consortia and across varied national contexts, it is difficult to enforce agreed upon rules, even though funding institutions and journals might have some leverage to demand best practices.

I believe that a critical science studies perspective on issues of racism and exploitation in microbiome research on hunter-gatherers, or Indigenous populations in general, can benefit from considering the history of hunter-gatherer studies and its internal debates in various ways. It might help to

- understand how microbiome research is driven towards evolutionary primordialism due to a sense of crisis of late modernity, this time less related to disenchantment and the nuclear bomb, as to a perceived health crisis and anthropogenic climate change (Lavi et al. 2024; Wilmsen et al. 2009).
- trace divides between microbiome researchers and the origins of different attitudes and sensibilities, with some researchers connected to the hunter-gatherer studies tradition, while others, coming from genomics and biomedicine, are not.
- see more nuance, especially in the work of anthropologists: Schnorr et al. (2014), for instance, makes problematic ascriptions but is full of hedging and qualifications, which are certainly informed by the critical stances to treating living hunter-gatherers as isolated analogs of ancient populations.
- find resources to more explicitly articulate, for specific (post-)hunter-gatherer groups, what De Wolfe et al. (2021) call associative factors and structural drivers, as these will concern many aspects that have been studied by revisionist anthropologists. By the same token, being explicit about the way in which populations are not isolated and live in environments that are different from precolonial environments can empower Indigenous activists in their negotiation of rights related to research and other issues.

However, the critical assessment of the category of hunter-gatherer that crystalized in the revisionist controversy, while being present throughout the history of hunter-gatherer studies, was at the core about methodology, and about the kind of data that was gathered and how it could be interpreted. Hence, I suggest an additional, epistemological issue to be addressed in hunter-gatherer microbiome research in the light of the history of hunter-gatherer studies.

The main contestation of the revisionist critique was that contemporary populations and their predecessors were influenced by global and local history. To downplay these effects through a rhetoric of traditional or ancestral lifeways will lead to bad science. Even though Schnorr and Crittenden initially used this rhetoric (Schnorr et al. 2014), together with their coauthors they contend that “[e]very population that is studied in the 21st cen-

tury is contemporary and influenced by the global economy as well as the nation state; to suggest otherwise is ... scientifically inaccurate (and overlooks important ecological variables that should be measured)" (Mangola et al. 2022, 752). Also here, the long-standing debates in hunter-gatherer studies can help further articulate this insight. These debates make clear that

- there can be no model population, as there is diversity geographically as well as temporally; this is due to significant differences and changes in environments—hence, there can be no such thing as the typical hunter-gatherer microbiome that could be compared with industrial microbiomes.
- there is, additionally, great variation in cultural features of groups identified as hunter-gatherers, regarding the complexity of social organization or the degree of sedentary life; furthermore, there are symbolic and religious aspects to the culture that are in turn different for each studied group. Hence microbiome research needs to take these factors into account, as they shape many aspects of hunter-gatherer lifeways, from division of labor to child rearing, food choice, and food preparation, that strongly affect the microbiome.
- hunter-gatherers have not (at least for the last few thousand years) been isolated; they have often been engaged in labor for and exchange with herders or agriculturalists, or in pursuing small-scale herding or horticulture themselves, and they have often been subject to violence, pollution, or medical interventions. Here, too, all these aspects will influence the microbiome and need to be investigated, documented, and considered in microbiome studies.

The focus on hunter-gatherers is clearly motivated by the special status of this mode of subsistence as primary in terms of human evolution. In biomedically oriented studies, the tenets of Darwinian medicine are always in the background and contemporary populations identified as hunter-gatherers are thus seen as providing information about the EEA and the respective physiological responses, including symbiotic relationships with microbiota. As debates in hunter-gatherer studies make clear, however, different Paleolithic hunter-gatherer populations have lived in diverse environments and in environments different from those inhabited by contemporary foragers. In addition to the variation in today's (post)foraging societies noted above, these issues undermine attempts to establish models of microbiome acquisition, composition, and function that represent generalized ancient conditions in which humans were well adapted to their environments, and that can inform medical interventions *on these grounds*. Moreover, the notion of maladaptedness inherent to Darwinian medicine can be contested, because it assumes that evolution is too slow to catch up with the fast pace of human cultural development. Yet in the light of the many evolutionary processes recognized today beyond changes in gene frequencies, this view cannot be upheld (Dupré 2012, Ch. 14). Most notably, for instance, microbiota evolve fast, through horizontal gene transfer (Groussin et al. 2021). Hence, the microbiomes of members of industrialized societies, even if they are less diverse, might still be adapted to the respective recent lifestyles. Low microbiome diversity is correlated with a higher prevalence of certain diseases. Nonetheless, attempts to attribute these prevalences primarily to dysbiotic microbiota are reminiscent of the ear-

lier attempts to ascribe all disease susceptibility primarily to genetic variation that were prominent in the context of the Human Genome Project (Darrason 2017).

Studies in evolutionary anthropology make use of the analogy between contemporary and ancient hunter-gatherers to learn about the latter. While these researchers tend to be closer to hunter-gatherer studies and hence show more awareness of the long-standing debates on the legitimacy of such analogies, it is not sufficient to introduce some caveats about the uncertainties of such inferences. Such analogies have to be justified separately for each property for which inferences are made. This follows clearly from the fact that hypotheses generated by analogy need to be supported by independent evidence (Lane 2014; Wylie 1985). Tool-use in ancient or contemporary hunter-gatherer populations might exhibit different patterns of similarity and difference than, say, kinship structures, and the evidence to support each claim would be very different. Hence research on microbiomes of contemporary populations aimed at understanding the biology of ancient populations needs to be more explicit about the reasons for assuming that analogical inference would be justified in each particular case. This requires specific competencies and knowledge that need to be acquired through learning or collaboration between evolutionary and paleo-anthropologists: 1) on specificities of the evolution of symbiosis and microbial communities; 2) on cultural specificities and local histories of interactions; and 3) on how the factors in (2) might affect the microbiome.

Many in hunter-gatherer studies see the category of hunter-gatherers as having more pragmatic value, rather than carving out a natural kind. The category is useful to orient research in archaeology and anthropology on populations with little to no herding or horticulture activity. Furthermore, it provides grounds for comparing very heterogeneous populations along the lines of shared themes to find family resemblances, but also, more importantly, interesting differences in need of specific local explanations. I suggest that this is an attitude that microbiome researchers should adopt, as well. Here, too, one can expect a complex network of similarities. More worthwhile will be the study of differences in microbiome composition and function in different hunter-gatherer populations (past and present) and their correlation with differences in the respective environments, histories, and ways of life. If, instead, the only outcome, driven by a desire to generalize, is that hunter-gatherer populations in general have a more diverse microbiome than members of industrialized societies, then this branch of research does not add much to the already well-established fact that rural lifeways in less developed nations (according to the HDI) are correlated with higher diversity in the microbiome. Given that such research adds to the threats that the studied populations face from expanding agricultural, extractive land use, and tourism, such weak results might not balance the negative effects (Gibbons 2018; Mangola et al. 2022).

Conclusion

With this chapter, I complement a growing body of critical science studies literature on race in microbiome research. My focus is on the use of the category of hunter-gatherers in this area of research. Science studies scholars have pointed to political and ethical issues in this field, including racism and representational violence, as well as exploitation

and bioprospecting. I have offered a brief summary of the history of hunter-gatherer studies and its internal debates on its central categories. I argue that awareness of these debates can lead to more depth and nuance in critical approaches, especially where they aim to improve the research. Additionally, it highlights another line of critique focused on epistemological questions. I have outlined this problem to set the stage for further discussion.

With regard to the questions that motivate this volume, the chapter has discussed some of the consequences of categorizing populations as hunter-gatherers (which might apply to other designations such as “pastoralists,” as well). The category scheme of modes of subsistence, to which the concept of hunter-gatherer belongs, is different from race or ethnic categories. Yet the respective classification systems strongly interact. As a result, designating populations as hunter-gatherers can, under certain circumstances, contribute to racialized injustice. Additionally, using this category can lead to methodological errors in research, affecting not only the researchers but also the groups that participate in research. Hence, microbiome researchers are well advised to listen to and engage with participant communities. As everywhere, unquestioned assumptions can lead to injustice as well as to poorly justified scientific claims. Microbiome researchers certainly discuss methodological issues, and increased interaction between this group with cultural anthropologists will lead to self-correcting processes of mutual critique. Nonetheless, science studies scholars can clearly contribute to making research sounder, not least by facilitating the transfer of knowledge between hunter-gatherer studies and microbiome research.

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