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Does the human microbiome tell us something about race?

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This paper critically discusses the increasing trend in human microbiome research to draw on the concept of race. This refers to the attempt to investigate the microbial profile of certain social and ethnic groups as embodied racial traits. Here, race is treated as a necessary category that helps in identifying and solving health challenges, like obesity and type-2 diabetes, in 'western' or indigenous populations with particular microbial characteristics. We are skeptical of this new environmentalist trend to racialize human bodies due to two reasons: (i) These race studies repeat outdated historical narratives, which link especially nutrition and race in ways that are prone to stir stereotypical and exclusionary views on indigenous groups. (ii) The concept of biological race used here is taxonomically problematic and conceptually inconsistent. It leads to a view in which human races are constituted by other non-human species. In addition, this approach cannot group biological individuals into human races and decouples races from ancestry. To support this critique, we draw on case studies of microbiome research on indigenous groups in Latin America.

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Introduction

The presence of race in biomedical research has been a long-contested issue. Social science scholars, as well as historians and philosophers, have voiced a number of concerns about the central role of race in human diversity research, the Human Genome Diversity Project and in genetic ancestry testing (M'charek, 2005; Tallbear, 2013; Lipphardt, 2014). In these approaches alleged racial differences are conceptualized as genetic differences. In the last two decades, we have seen increasing trends to move away from gene-centered views on development, physiology and health, and towards more environmentalist views. At first sight, these shifts also include abandoning a biological concept of race. However, this assumption is illusive (see Duster, 2015). In recent years, postgenomic developments in fields like epigenetics and neuroscience have led to new environmentalist ways to link the social-cultural and economic status of certain ethnic groups with their disease susceptibilities, especially for obesity and type-2 diabetes (see Meloni, 2017). This biosocial view of human differences ultimately defines biological characteristics, such as epigenetic (gene expression) patterns, as embodied racial patterns (see Kuzawa and Sweet, 2009; Baedke and Nieves Delgado, 2019). The most central mediators of such racial embodiments are stress, environmental toxins, lifestyles, and nutritional habits.

As part of this general trend, human microbial ecology in particular has recently seen a rapid increase in the use of racial classifications in explicit or implicit ways. This research draws on the fact that human bodies consists of at least as many microbial cells as human cells (Sender et al., 2016). The human microbiota includes all those bacteria, archaea, fungi, protists, and viruses that colonize, among others, humans' skin, placenta, uterus, seminal fluid, lung, saliva, oral mucosa, conjunctiva, and especially their gastrointestinal tract. The collection of all genomes of these microorganisms is called microbiome. It is housed by a 'holobiont,' i.e. an integrated collective of multiple species (Gilbert et al., 2012; Rosenberg and Zilber-Rosenberg, 2016). Microbiota have become a central research target to understand how socio-environmental factors, especially lifestyles, nutrition, and the use of antibiotics, affect normal development, pathologies, and diseases, from diabetes, obesity, and asthma, to cancer and neuropsychiatric disorders (e.g., Durack and Lynch, 2019; Zmora et al., 2019). In this field of research, race is a classificatory framework that should allow understanding disease susceptibilities of particular human populations. It is assumed that groups considered to be racially different show a characteristic social-cultural profile that is embodied as a specific make-up of microbial taxa living closely linked with humans, which in various ways affect their health.¹ In short, racial difference is conceptualized as socio-cultural difference that is inscribed into human holobionts.

Amber Benezra (2020) recently criticized this trend in human microbiome research to racialize human bodies and socio-cultural differences. She argues that race is used as a problematic 'ghost variable' in the field and that social scientists should be more seriously involved into transdisciplinary collaborations with microbiome researchers to put microbial differences into perspective and address racial health disparities (see also Greenhough et al., 2020). By building on and expanding Benezra's (2020) criticism, we seek to highlight the historical and conceptual pitfalls that this new race-based approach falls into when trying to biologize human cultural diversity. The paper, first, discusses how human microbial ecology studies host-microbiota collectives (section "Humans and their microbiome") and how the field tries to implement race as a category for identifying health issues of certain human groups (sections "Race in human microbiome research" and "Race and the microbiome in Latin

America"). Here, we address the empirical and methodological problems of this research. Second, two reasons are presented for why this research is poorly motivated and questionable in historical and conceptual ways. On historical grounds, we shown that (i) microbial race studies reintroduce problematic environmentalist narratives (from colonial humoralism and acclimatization debates), linking especially nutrition and race in ways that are prone to stir stereotypes about indigenous groups (sections "Environmentalist views on race in historical context" and "Nutrition, civilization levels, and research populations"). On conceptual grounds, we argue (ii) that the concept of race used in the field is taxonomically and conceptually inconsistent and ultimately leads to a counterintuitive view of human races. This view, according to which human races are constituted by non-human (microbial) taxa, cannot group biological individuals into races in taxonomically meaningful ways, and decouples race from ancestry (sections "Biological individuality and taxonomy" and "The race of the holobiont"). To support this critique, we draw on case studies of microbiome research on human populations in Latin America.

Humans and their microbiome

In the past 15 years, the microbiome has become a target of various research projects in the biological and biomedical sciences. This development has been driven by the finding that in many species symbiotic microbes can play crucial roles by providing selectable variation and biasing the evolution of their host (Brucker and Bordenstein, 2013; Gilbert, 2020), and by transmitting information across generations (Gilbert, 2014; Browne et al., 2017). In particular, studies in animals and humans showed that microbes can be central agents that affect normal development. For example, they allow for the normal development of the immune system and the gut capillary network in mice (see Gilbert et al., 2012). In addition, germ-free mice develop asocial and autistic-like behaviors (Desbonnet et al., 2014). This phenotype can be replicated by transferring the microbiome of autistic human patients to germ-free mice (Sharon et al., 2019).

In humans, numerous microorganisms play various roles in health and disease (see Wang et al., 2017). The human microbiome has been associated, among others, with autoimmune diseases (Wen et al., 2008), respiratory diseases (Verhulst et al., 2008), and metabolic disorders, like diabetes mellitus, metabolic syndrome, and obesity (Wang et al., 2017). The gut microbiome in particular seems to play a crucial role in human health (Zmora et al., 2019). Among others, gut microbes co-modulate the metabolic phenotype, epithelial development, and the host's immune system (Macpherson and Harris, 2004), and can contribute to mental health and disorders, like depression, via the so-called 'gut-brain axis' (Clarke et al., 2013).

Such findings suggest that biological normality is not intrinsic to organisms but arises through relations with other organisms. While traditional western understandings of health see bacteria as deviations from the norm that contaminate the individual's physiological equilibrium, in the microbial framework, microbes make possible normal development and can prevent certain diseases.

The recently (re)introduced concept of the *holobiont* (i.e. an integrated composite unit of microbial and host eukaryotic species) allowed organizing much of this new microbial data (Gilbert et al., 2012; Rosenberg and Zilber-Rosenberg, 2016; Baedke et al., 2020; Baedke and Gilbert, 2020). It offered a framework to look at the complicated roles microbes play in affecting human health. This complex picture of the human holobiont is even more expanded when factors such as sex and

age of the host and socio-cultural and economic factors are taken into consideration, which can cause health-related changes in microbial diversity and composition. The latter set of factors can be as diverse as lifestyle, physical activity, dietary habits, hygiene, birth and breastfeeding practices, socio-economic status, urbanization, health care access, and antibiotic usage (see He et al., 2018; Porras and Brito, 2019; Quin and Gibson, 2020; see also Benezra, 2020). One variable recently added to this set is the host's ethnicity and race.²

Race in human microbiome research

From 2007 to 2016, the NIH Human Microbiome Project investigated whether differences in microbiome ecology and health-related outcomes are associated, among others, with (self-reported) ethnic, racial, and national categories, such as Black, White, Asian, Mexican, and Puerto Rican. One of their project reports concludes that “ethnic/racial background proved to be one of the strongest associations” of metabolic pathways and microbes with clinical metadata (Huttenhower et al., 2012). While this study did not explore the causes of these associations, one could assume that the observed microbial differences are due to racial belonging of participants (see Fortenberry, 2013). These and similar findings have triggered various studies that further explore the potential connection between race and microbial ecology. These studies, published in influential journals in the field, usually link groups that are considered to be human races and their health status with geography-specific, nationality-specific, and/or lifestyle-specific variations in microbiomes in the oral cavity, respiratory tract, skin, urogenital tract, and in the digestive system (see Benezra, 2020, p. 883). Among these, especially the gut microbiome is considered to show the largest diversity between different racial groups (see Gupta et al., 2017).

While these studies often lack a precise definition of what they take race to be (or even do not use the term but apply racial categories, like African American or Latino), the explanatory role the concept (or racial category) plays in these investigations usually is quite clear. Race emerges in human microbiome ecology as ‘biosocial race’ in which socio-cultural diversity in human groups is taken to induce differences in health-related biological traits in these groups. At the same time, the biological component of race (understood as difference in microbial characteristics of groups) has some degree of autonomy from social factors, as it also depends on the host's genome and can be transmitted through biological (besides cultural) inheritance channels.

There are currently two seemingly opposing kinds of race studies with different explanatory interests. First, one set of investigations focuses on developing interventions for traditional, indigenous, or non-western populations with seemingly high disease susceptibilities. These populations, often in or coming from the ‘Global South’ (shorthand to include postcolonial areas outside Europe and North America), have become the target of microbiome-focused health disparities studies (Findley et al., 2016; Gupta et al., 2017). Here, usually certain socioeconomic, psychosocial, and behavioral factors as well as diet are considered to characterize racial groups with higher disease susceptibilities. For example, studies have linked higher rates of adverse pregnancy outcomes, infections, and bacterial vaginosis in black and Hispanic woman in the US with differences in the vaginal microbiome (Fettweis et al., 2014; for discussion, see Benezra, 2020). Another study tries to explain the higher prevalence of obesity and type-2 diabetes in Mexican Americans through lifestyle-related changes in microbial network relationships (Ross et al., 2015). In such studies the indigenous or non-western microbiome is often characterized as disease-prone and at-risk and, thus, in need of treatment. Here, the use of racial categories

is usually legitimized through the aim of solving severe health issues in underdeveloped nations and certain social groups.

A second, even faster growing set of studies focuses on the ‘impoverished western microbiome’. In these studies, the subtending assumption is that in the evolution of the human microbiome the diversity of microbial species decreased, when human ‘civilizations’ passed from foraging and rural farming to urban and industrialized western lifestyle that includes overuse of antibiotics and high-fat diets (e.g., Clemente et al., 2015; Segata, 2015; Vangay et al., 2018; Zuo et al., 2018; Sonnenburg and Sonnenburg, 2019). In short, along a spectrum from primitivity or traditional purity to westernization or urbanization, racial groups are placed together with their more or less diverse microbial ecology. In this view, chronic ‘western diseases,’ like obesity, are understood to be caused by a misbalanced (so-called dysbiotic) ‘urbanized’ microbiome, which can be induced, for example, through high-fat diets and overuse of antibiotics. In order to overcome these diseases, we should, so the argument goes, ‘rewild’ our gut microbiome by reintroducing missing microbes dominant in traditional populations (Blaser, 2014; see also Lorimer, 2017; Hobart and Maroney, 2019).³ These studies usually operate with highly idealized assumptions about the purity, isolation, and uncontactedness of indigenous groups (see Maroney, 2017; Benezra, 2020), which are instrumentalized for the purpose of saving the ‘western gut’. For an example of how traditional groups are depicted in these studies, see Fig. 1.

Both kinds of studies may attach quite different values to human groups, some of which are diametrically opposed, for example, when framing non-western groups as overly healthy or permanently at-risk and sick. However, both narratives may also be integrated in one and the same investigation, for example, on shifts in the microbiome of non-white, non-westernized populations who migrate to an urbanized environment. Then, usually, the once pure and healthy traditional microbiome gets distorted, decreases in diversity, and ultimately leads to higher disease susceptibilities (even higher than those of western microbiomes). An example is a study linking the migration of “ethnic” groups from a “non-western country”—Hmong and Karen groups living in mountain regions in Thailand—to the rapid loss of native strains and diversity of gut microbes (starting upon arrival), the loss of bacterial enzymes associated with plant fiber degradation, and a transition from *Prevotella* to *Bacteroides* dominance (Vangay et al., 2018, p. 962). This shift in races through westernization, “in which US-associated strains and functions displace native strains and functions”, is taken as a cause for high rates of metabolic diseases in US immigrant populations.

So far this use of racial classifications in microbial research has raised surprisingly little concern (but see Hobart and Maroney, 2019; Benezra, 2020). Within the scientific community, only few review articles ask researchers to be more critical about the use of racial categories as proxies for true causes of diversity in the microbiome (Fortenberry, 2013; Findley et al., 2016). However, even these studies do not fully reject a usage of the concept or try to provide alternatives to racial categories. In this paper, we take a more critical stance. In face of the danger to biologize social constructionist understandings of race in human microbial ecology, we urge scientists in the field to reflect on whether they understand racial difference as a social or, in fact, biological reality, and to avoid race entirely when it comes to describe *biological* diversity of humans. This is due to empirical, historical, and conceptual reasons.

On empirical and methodological grounds one should be skeptical about whether correlations between microbial diversity, health, and cultural factors really hint towards embodied racial patterns of variation. We currently see conflicting reports that highlight specific nutrients, metabolites, and microorganisms as



Fig. 1 Representation of human populations' transition from primitive to urbanized. The figure states that a cultural change from foraging and rural farming to urbanization and industrialization goes along with a decrease in microbial diversity (Gupta et al., 2017).

both beneficial and detrimental to the health of the host, with race sometimes seeming to play a role and sometimes not (see Gupta et al., 2017; Quin and Gibson, 2020). This could stem from methodological differences between omics-approaches and high levels of inter-individual (and even intra-individual) microbial variations (Ursell et al., 2012; Jones et al., 2018).

Another empirical problem is that many human health studies are currently inspired by results in rodents. However, extrapolations from these models have been found to overstate the causal role of the microbiome in human diseases stirring unrealistic expectations (Walter et al., 2020). In addition, we should not necessarily assume that other species' microbiome is comparable to that of humans, is transmitted in similar ways, or plays similar roles in health and disease. For example, the microbiome of lab mice differs from that of wild mice, thus making it a poor proxy for understanding human microbiota (Rosshart et al., 2019). In addition, in many species microbes do not play the central causal roles we would like to attribute to them in humans. Surprisingly, some wood eating crustaceans do not have gut microbes (Boyle and Mitchell, 1978), nor do caterpillars have a resident gut microbiome (Hammer et al., 2017). Some ant species have 10,000 times more gut microbes than others, without clear differences in diets (Sanders et al., 2017). Such results do not draw a picture of the microbiome that is taxonomically and functionally specific and stable for a certain group of hosts, in contrast to what race-based human microbiome studies want to tell us.

Based on these empirical problems, biologists and philosophers of science have cast doubt on the strong causal role of the microbiome in human health and development. Especially in cases of obesity and mental health explanations, microbiome causality merely shows low stability and specificity (Lynch et al., 2019). Thus, against catchy slogans like 'you are what you eat' (Zmora et al., 2019, p. 25), which might stir hopes for personalized or group-specific health interventions, we should rather question whether recent human microbiome discoveries really have far-reaching effects on our understanding of our biological identity, our 'self,' and what it means to be human (Parke et al., 2018).

Besides the above empirical concerns against the use of racial categories to classify human microbiomes and their health effects, below we present two further critical arguments. They concern historical and conceptual problems associated with the use of a biologized concept of race in this research context. By historically

contextualizing human microbiome research, we show, first, that microbial race studies reintroduce outdated and stereotypical environmentalist argumentative patterns from humoralism and acclimatization debates (sections "Environmentalist views on race in historical context" and "Nutrition, civilization levels, and research populations"). Second, through conceptual analysis, we reveal that these studies operate with a conceptually inconsistent view of race that struggles with the grouping of biological individuals into human races (sections "Biological individuality and taxonomy" and "The race of the holobiont").

To illustrate these historical and conceptual points, we draw on microbial race research in Latin America on, among others, indigenous groups, Hispanics, *mestizos*, and Mexicans.⁴ After systematically reviewing recent microbiome literature on these groups we identified a set of representative studies in the field (see below) based on the following criteria: use of biologized racial/ethnic or national-geographic categories, application of contrastive frameworks that distinguish human populations in (or from) Latin America from westernized or urbanized populations, and impact in the field. Then, central narratives in these studies about body-environment relationships, nutrition, and environmental effects on health were compared to environmentalist narratives applied on the same populations (especially indigenous groups) in Spanish chronicles of the New World (16th to 18th century) and acclimatization debates (19th to 20th century) to trace continuities or reoccurring argumentative patterns. Moreover, we analyzed the consistency of the conceptual framework underlying these narratives in microbiome research, particularly with respect to how they link the concept of race to biological taxonomies and biological individuality.

Race and the microbiome in Latin America

In recent years, race or ethnicity studies on human microbiomes in Latin America have been rapidly growing.⁵ They have been motivated, in line of the two research strains described above, by the attempts to understand how a dysbiotic or unbalanced microbiome is linked to social and health disparities or to identify indigenous non-westernized microbiomes. For example, in 2015, 32,4% of the Mexicans adult population were obese (OECD, 2017) and the 'Mexican microbiome' has been suggested to contribute to this (Méndez-Salazar et al., 2018). Building on these

Table 1 Examples of microbiome studies on human populations in or from Latin America.

Number	Relationships studied	References
1	Gut microbial dysbiosis, type-2 diabetes, obesity, diet, and lifestyle in Latin Americans and the US Hispanic/Latino community	Romero-Ibarguengoitia et al. (2019)
2	Gut microbial diversity and composition, point in life of relocation of Latinos (Hispanic national origin) to the US, lifestyle (diet, physical activity habits) and obesity	Kaplan et al. (2019)
3	Oral microbiota composition and obesity-linked diseases (like diabetes, uncontrolled hypertension, and cancers of the stomach, and liver) in Mexican American women, and their level of acculturation	Hoffman et al. (2018)
4	Variation in oral (subgingival) microbiome, chronic periodontitis, and type-2 diabetes in Mexican Otomí Indians compared to Mexican <i>mestizos</i>	Rodríguez-Hernández et al. (2017)
5	High bacterial and functional diversity of gut, skin, and oral microbiota (and presence of antibiotic resistance genes in microbiome), and hunter-gatherer lifestyle in a 'isolated Yanomami Amerindian village [Venezuela] with no documented previous contact with Western people', compared to Western microbiomes (incl. potential treatment of antibiotic resistance in Western populations)	Clemente et al. (2015)
6	Decrease in core genera in a 'Western dataset' (Flemish, Dutch, UK and US populations) compared to populations of Peru	Falony et al. (2016)
7	Bacterial assemblages and functional gene repertoires in children and adults from the Amazonas of Venezuela and US residents	Yatsunenko et al. (2012)
8	Gut microbiome structure of rural agriculturalists from Venezuelan Amerindians compared to that of Hadza (Tansania), Malawians, and South Africans	Gupta et al. (2017)
9	Gut microbiome composition of extinct populations (Caserones in northern Chile (1600 years B.P.) and Rio Zape in northern Mexico (1400 years B.P.)) and microbiome of today's uninidustrialized rural communities, in contrast to the microbiome of cosmopolitan communities	Tito et al. (2012)
10	Gut microbiome structure in different hunter-gatherer populations (e.g., 'traditional people' from South America) and those of traditional rural agriculturalists (e.g., Amerindians from Venezuela) and of European and North America urban industrial populations	Obregon-Tito et al. (2015)
11	Oral microbiome composition (in saliva and subgingival biofilm) between populations of US Latinos, compared to non-Hispanic whites, non-Hispanic blacks, and Chinese living in the US (incl. attempt to identify an individual's ethnicity from oral microbial signatures via machine learning)	Mason et al. (2013).
12	Vaginal microbiome composition of different ethnic North American groups (Hispanic, white, black, and Asian)	Ravel et al. (2011)
13	Skin microbiome of Amerindians in the Venezuelan Amazonas (recently transitioned from a nomadic hunter-gatherer lifestyle to permanent homes with access to certain aspects of modern life, yet with a relatively traditional diet) and of healthy persons in New York and Colorado	Blaser et al. (2013)

and similar observations, various studies (attempt to) establish relations between microbiota, the hosts' health and cultural or racial parameters in Latin America (see Table 1, numbers 1–4). Besides these health-disparity studies other investigations focus on 'primitive' and 'westernized' microbiomes in Latin America (see Table 1, numbers 5–13).

Latin America is seen as ideal playground for these studies, as it is not only home to non-western lifestyles (especially assumed-to-be-uncontacted hunter-gatherer populations), but also displays high diversity of host genetics (due to the countries' colonial history), and populations with high prevalence of chronic diseases such as obesity (Cornejo-Granados et al., 2019, p. 236). In other words, it presumably provides access to health-relevant ethnic and racial diversity.

Microbiome studies on populations in Latin American create specific narratives about people, lifestyles and bodies: First, narratives about deprived indigenous and *mestizo* bodies in developing countries or with traditional lifestyles that become sick and are at-risk; second, narratives about the purity and primitivity of uncontacted indigenous groups that are decoupled from a western lifestyle. In both kinds of narratives especially nutrition and changes in life-style or location play a central role. As we show now, these microbial narratives are not new, however. They show strong similarities with argumentative patterns in old colonial and racial debates about humoralism and acclimatization in the region.

Environmentalist views on race in historical context

Nutrition, environment, and race have long been coupled in various ways.⁶ In relation to health, an influential account was humoralism, a Hippocratic-Galenic medical doctrine introduced

to the Americas during the Conquest (Davies, 2016; Earle, 2013) that remained relevant well into the 20th century in acclimatization and degeneration debates (e.g., in medical geography; Rupke, 2000). It assumed a close relation between a highly permeable body and a varied collection of factors to be found in its surrounding environment. In this view, bodily constitution, health and even personality were related to different humors, which were altered by the consumption of certain foods, the exposition to climatic factors and the regularity of habits (see Glacken, 1967; Foster, 1994).

In this framework the bodies of indigenous or *mestizos* were 'racially' distinguished from that of Spaniards. Here, like contemporary views emerging in human microbiome ecology, race was not considered intrinsic to bodies but as a body–environment relationship whose stability depended on maintaining habits and nutrition (Baedke and Nieves Delgado, 2019). Accordingly, health was an environmentally influenced balance state linked to a specific place and behavior. The accidental or induced loss of humoral balance by change in climate, diet, or habits could lead to disease and even death. An example of the effects of change is the report of Martín Fernández de Enciso, who attributed the death of indigenous people from the Yucayas (today Bahamas) to relocation and diet change from fish, roots and grass to meat (see Gerbi, 1985, p. 87). Similarly, according to Columbus, the death of 200 *indios* brought by him to Europe was the result of a change from warm to cold climate (see Morrison, 1963, p. 227). In general, *indios* and Europeans were believed to have different humoral constitutions and thus dietary requirements. For instance, *indios* (phlegmatic) could nourish from chilli (*chile*) but this plant would cause diarrhea in Europeans as they had a choleric constitution (de Cárdenas, 1913 [1591], p. 115).

This environmentalist view of body difference and health was strongly linked to a hierarchical view on civilization. For instance, de Cárdenas (1913, p. 176) argued that the permanent exposure to heat and moisture of such environments “produces filthy and dirty subjects such as indios and blacks” and fostered diseases more than other places. Accordingly, bodily characteristics of indigenous were increasingly described as degenerated, sick, and at-risk. This pejorative view of the native populations would become standard by the end of the 18th century with the works of Georges-Louis Buffon, and later, Cornelius de Pauw (see Glacken, 1967; Gerbi, 1985; Cañizares-Esguerra, 2006). The link between primitive bodies, local environments, habits, and nutrition, and low health states or higher disease susceptibilities, stirred fears of degeneration among Spaniards living in the colonies (see Gerbi, 1985; Cañizares-Esguerra, 2006; Earle, 2013). This perspective was based on stereotypical categorizations of bodies and behaviors, such as, civilized-primitive, healthy-ill, and advantaged-deprived, which not only led to a hierarchy of races. It also ranked certain local body–environment balances as desirable or undesirable, forcing settlers to continuously take care of their malleable bodies through well-aligned life strategies to prevent degeneration and sickness.

Ongoing colonial activities of Europeans fostered the popularity of environmentalist views of race, especially in discussions on acclimatization (Livingstone, 1987; Heggie, 2019). The main question about acclimatization was whether the European body can preserve its health when relocated to another abnormal (tropical or extreme) non-European environment (Livingstone, 1991). According to this account, bodily differences (skin and hair color, skeletal and head structure) were racial cues that resulted from environmental acclimatization (Livingstone, 1987). People with non-European traits living in colonized spaces were seen as deviating from the civilized norm. In general, this debate mixed ideological views on what was considered primitive and civilized races with scientific positions of the time on the origin of human diversity (monogenism and polygenism) and the possibility of change (see Huntington, 1915; Deniker, 1913).

In the context of the Americas, the discourse of acclimatization was employed mainly to make sense of the physiological differences between indigenous populations and the incoming European settlers. Indigenous bodies were usually conceptualized as resulting from the harsh or undesirable climatic conditions during development and from their nutritional habits (Turda and Gillete, 2014; Vargas-Domínguez, 2017). They were considered to require special diets to compensate their deficient upbringing and to ascend in the racial scale. By drawing on these environmentalists’ views, the racial betterment of indigenous bodies became a focal point of Latin American eugenics (Pohl-Valero, 2014; Knight, 1990). In these narratives, nutrition played a key role to link race and civilization hierarchies as well as describe stereotypical body–environment balances in lower and higher races (incl. health risks through distorted balances).

Nutrition, civilization levels, and research populations

During the 19th and 20th century, food “evolved into a material instrument of statecraft” (Cullather, 2007, p. 338; see also Shapin, 2014) and the body was increasingly understood as an energy burning machine. These two new developments allowed governments to prescribe dietary regulations, measure energy consumption, and compare nutritional states between nations, classes, and races (Cullather, 2007, pp. 341–342). Intellectuals in Mexico, Colombia, Brazil, and Argentina (see Bulnes, 1899; Roldán, 2010; Pohl-Valero, 2014) developed frameworks that connected nation-building projects to local eugenic movements and incorporated but also reshaped scientific ideas of metabolism.

In these works, indigenous bodies were considered problematic, as they were energy-inefficient and in need of racial improvement (see, e.g., Pohl-Valero, 2014, p. 464).

Racial inferiority was assumed as well as empirically proved by performing physiological measurements, for example, on metabolic rates. These measurements used foreign standards (mainly European and North American) as default. Higher indigenous metabolic rates, such as those measured in the Mayas from Yucatán and the Araucanian Mapuches (Benedict, 1937, p. 104) were treated as anomalies induced through specific behaviors and nutritional patterns. The scientific corroboration of an indigenous “altered metabolism” (Vargas Domínguez, 2017, p. 576) stirred and justified the study of these human groups into the present. These groups were increasingly considered as representatives of an early primitive evolutionary state in human’s biological and cultural history whose study could reveal physiological characteristics that cannot be found in the western world.

Anthropological, physiological, population genetic, and epidemiological studies on these ‘primitive bodies’ have focused on a selected set of indigenous groups, like the Otomí and Pima (in Mexico), Yanomami (Venezuela and Brazil), and Kayapo (Brazil), whose metabolism and diseases susceptibilities have been extensively studied (Trowell, 1975; Knowler et al., 1983; Neel, 1970, 1972). These studies tend to take a particular indigenous group as proxy for describing every other group. By doing so they are prone to promoting a distorted and stereotypical view of indigenous biologies as homogeneous, primitive, (evolutionarily) static, and in danger of disappearance. This problem resurfaces in current microbiome research.⁷ Again the same populations are studied through the old lens of environmentalist racial classifications.

One example of this is current microbiome studies on Otomí in Mexico. This group was selected as early as 1936 as object of study, because they were considered by ethnologist Jacques Soustelle as the “most primitive men” to be found (Vargas Domínguez, 2017, pp. 571–572). Back then, Otomí nutritional habits and metabolic characteristics were evaluated against Caucasian standards. Their higher metabolic rate was interpreted as less efficient, like a motor that needs more or better fuel. These results informed social programs of diet improvement to modify the “primitive behavior” of the Otomí people and their racial transformation into *mestizos* (see Vargas-Domínguez, 2017). Today, the Otomí are still an object of study—and their bodies are still considered prone to diseases. Current microbiome studies contrast Otomí subgingival microbial profile with that of Mexican *mestizos*, in both cases with and without type-2 diabetes (Rodríguez-Hernández et al., 2017). The study presupposes that “[i]ndigenous and urban Mexican populations” occupy “different geographical locations and have distinct cultural, nutritional, and healthcare regimens”, which explains the high prevalence of type-2 diabetes and periodontal disease in Otomí. The study suggests that the higher predisposition for periodontal diseases found in Otomí is linked to their microbial profile. While the authors do not suggest racial differences or hierarchies, they implicitly build their argument on idealized views on indigenous bodies as untouched and (at least to some degree) pristine, which reify the category of ‘indigenous’ (see López-Caballero, 2018).

Another example are studies on Yanomami in Venezuela. While the Yanomami are studied intensively since the 1950s (see Neel, 1972), current microbiome research is still treating them as “an uncontacted community [that] therefore represent[s] a unique proxy for the preantibiotic era human resistome” (Clemente et al., 2015).⁸ In the last 70 years the Yanomami have changed from being exemplars of a ‘thrifty genotype’ (famously by James V. Neel) with high susceptibility for metabolic disorders and obesity, to carrying a pristine bacterial gut, skin, and oral

diversity, whose understanding might allow “reverse the current global trends in metabolic and inflammatory diseases” (Clemente et al., 2015) induced through the overuse of antibiotics. In short, Yanomami have changed from being sick to saviors. However, their stereotypical characterization remains unchanged. They are still primitive, decoupled from western lifestyles, and frozen in evolutionary time in their pure biological state. Thus, Neel’s original view on them still holds in the microbial age: “The world of primitive man is remarkably uncontaminated” (1970, p. 820).

Recent human microbiome studies tend to repeat such outdated and problematic environmentalist narratives, which link especially nutrition and race. They are prone to attach normative values to indigenous groups, their habits and bodies, and stir stereotypic comparative frameworks, like *civilized–primitive*, *globalized–uncontacted*, *normal–abnormal*, *pure–contaminated*, and *healthy–ill*. Human microbiome research draws on these old narratives about races’ balance of body–environment relationships, and how this balance can be maintained or restored. Not all these narratives conceptualize the indigenous body as an exemplar of a sick race—in fact, it can be quite the opposite in microbiome studies. However, this historical review, from humors to microbes, should still be taken as a warning sign that microbiome research is following the argumentative patterns of exclusionary classifications of human diversity.

To strengthen our argument against the use of racial classifications in human microbiome research even more, we now reveal more fundamental flaws related to the conceptual framework underlying these race studies.

Biological individuality and taxonomy

A central presupposition of racial classifications in human microbiome ecology is that the human microbiome is highly specific for a certain group of individuals and qualitatively different between two groups of individuals. While this could be questioned on empirical grounds—as many microbiomes can be transient, display high inter-individual and intra-individual variation, and variation over time (Ursell et al., 2012; Jones et al., 2018)—we do not want to do this here. Rather we want to critically address the underlying conceptual framework that should legitimize grouping biological individuals into different races based on their microbiome. Therefore, we have to clarify the concept of *biological individuality* used here. There are two ways in which scientists in human microbiome ecology conceptualize human individuals in relation to their microbiota: (i) They consider microbes to *not* be an integral part of human biological individuals, but acknowledge that they are biological entities that carry information about individuals’ race, i.e. they are surrogates for human races; (ii) they consider the human microbiome to form an integrated collective individual together with the host, a holobiont, to which we can address a particular race. We will show now that both conceptualizations of race are theoretically inconsistent and counterintuitive.

Let us start with the first ‘microbiota as surrogates for races’ view. This view leads to a taxonomically highly problematic approach. Let us develop this argument in detail. If we assume some kind of biological similarity between humans and other species, we need to place any racial taxonomy of humans within a larger systematic framework depicting the relatedness of life-forms. Within Carl Linnaeus’ framework, biologists usually rank (geographical) races as subspecies (see Barbujani and Massimo, 2013). While race—in humans—can be given a social dimension and also occurs in folk-taxonomies, in biology it carries the idea that there are certain biological properties one particular subspecies has, which allow describing it as a race within a certain species.

In the history of biology and physical anthropology, the idea of racial grouping as a genuine taxonomic challenge has been present since the beginning. Linnaeus divided the human species into four subspecies, Johann Friedrich Blumenbach into five, and Georges Cuvier into three. While 19th and 20th centuries evolutionary theories shifted from typological to geographical and genealogical-genetic definitions of race, their rank within the taxonomic system largely remained unchanged. For example, the theory of human races as subspecies was defended by architects of the Modern Synthesis (see Jackson and Depew, 2017). Ernst Mayr (2002) argued that “before the voyages of European discovery and subsequent rise of a global economy” human subspecies were basically identical to races in the animal world (Mayr, 2002, p. 131).

However, in the last decades, this position, dominant especially in human population genetics, was increasingly challenged. Due to a growing understanding of the complexity of the human genome and the fact that the amount of genetic variation within each human population is substantially greater than between populations (e.g., Lewontin, 1972), an increasing number of biologists argued that the idea of human races cannot be given a useful biological, taxonomic meaning (Cavalli-Sforza et al., 1994, p. 19; Templeton, 2013). Despite this problem to describe human races as subspecies, some researchers still maintained that one can identify significant genetic patterns that allow a clustering and a continuous, non-discrete distinction of human populations (for discussion, see Pigliucci and Kaplan, 2003).

In line with earlier approaches, all these ongoing classification attempts share the idea of identifying biological, biomedical, and possibly even systematically meaningful populations located *below* the species level. For example, biologists group human populations based on certain frequencies of genes in them, which we consider characteristic for the genome of *Homo sapiens* (see Marks, 2003). They do not group individuals in different biological races according to entities located *above* the species level, like characteristics of Hominidae (e.g., walking upright), nor according to entities of *other non-human taxa* that could be considered to allow distinguishing human races. For example, we do not cite pets—dogs, cats—certain human populations keep in order to distinguish them as different biological human races. We have other non-biological classificatory systems for that, like ‘dog-people’ vs. ‘cat-people.’

This means that even most recent population genetic clustering of human races aligns, in some fundamental way, with our taxonomic system. This is because of the following reason: If this basic assumption is dropped, if biological entities from *any* systematic level (outside that of the human species) can be informative for racial differences—as surrogates for race—one can no longer defend the claim that, biologically speaking, belonging to a human race includes belonging to the human *species*. In other words, whether an individual belongs to a particular human race no longer provides information about this individual being part of the human species. Instead, it merely provides information on other non-human taxa.

Let us illustrate this problem with an example from human microbiome research. Mason et al. (2013) investigated oral microbiome composition (in saliva and subgingival biofilm) between populations of US Latinos, compared to non-Hispanic whites, non-Hispanic blacks, and Chinese living in the US. They attempted to identify an individual’s race from individual oral “microbial fingerprints” by using a machine learning classifier. They argue that this tool not only allows identifying an individual’s “ethnicity” from oral microbial signatures (e.g., in Latinos with a 67% sensitivity and 80% specificity). In addition, this approach should also be able to use the mere presence of a consortium of selected microbial species “as surrogates to predict

an individual's ethnicity"—all this, notabene, without knowing anything about the individuals' genome, nor about her socio-cultural background, habits, personal or work life.

This and similar microbiome studies defend a radical taxonomical position on race. They understand non-human species as central biological entities that allow racially grouping and distinguishing human individuals. This is a completely novel taxonomic view of biological races that was never before defended in the history of physical anthropology and evolutionary biology. Previous accounts never dropped the thesis that information on individuals' racial belonging has to be gathered *within* the human species, and that races reflect diversity *within* the human species. In contrast, human microbiome research defends the idea that belonging to a certain race, say Latinos, does not mean, strictly speaking, belonging to the human species, but showing some kind of biological relations with other non-human species, among others, bacteria of the genus *Prevotella*, that constitute an individual's race. In short, microbial genera living in and on Latinos biologically constitute their race.⁹

As we see, the first conceptual framework for how microbiota allow classifying biological individuals into races—microbes work as external, but informative surrogates of human race—takes a highly counterintuitive and taxonomically problematic stance. It holds that distinguishing human races entails no information about variation within the human species, but about variation in other taxa.¹⁰

The race of the holobiont

The second view on how biological individuals can be grouped in human races conceptualizes the microbiome as forming an integrated collective individual together with the host (see point (ii) above). This holobiont is then attributed a particular race, and grouped together with similar holobionts into racially distinguishable populations. However, as we will see now, this understanding of race is conceptually inconsistent.

Race, as understood in biology, refers to a property of individuals that, on its biological dimension, is inherited from generation to generation, thus allowing observers to identify an individual's race through her ancestry or genealogy. This is the idea that Latino parents have Latino children that not only 'look like them' but that are related to them. According to this theory of race, dominant in the history of biological and anthropological thought (see Marks, 2017) and in, often methodologically questionable, population genetic clustering (e.g., Ceci and Williams, 2009; Reich, 2018), biological races form lineages of individuals and share biological ancestry.

Can we, however, classify holobionts into races in the same ways, based on shared ancestry? For this, holobionts need to be reproductive individuals. In other words, this multicellular and multi-species system (host plus microbiota) needs to form a lineage that allows clear racial classifications. This would, for example, mean that all Yanomami Amerindian with the same gut microbial composition are members of the same lineage and have a common ancestor. However, this is far from being the case. Holobionts poorly qualify as reproductive individuals. In fact, in humans, the information stored in around 10–100 trillion microbial lineages is passed on in substantial ways independent from our genetic lineage, and not only vertically but also horizontally (Jeong et al., 2019). Thus, holobionts do not qualify as reproductive individuals, and they cannot be racially distinguished as such.¹¹

Due to this, we usually find several cross-cultural and cross-national similarities between microbially classified human races that do not (at least not directly) form lineages or biologically informative genealogies (see Quin and Gibson, 2020). Indigenous

groups living in quite different places, like Matsés in Peru and Hadza in Tanzania, share characteristics in their microbiome, like a higher diversity (Obregon-Tito et al., 2015). Another example is the high abundance of *Prevotella* in the gut of individuals from Peru and Malawi (see Gupta et al., 2017). But these similarities are not due to close ancestry that would qualify grouping them as one biological race, but, instead, correlate with shared life-style patterns and diet, "which clearly indicated that the influence of diet/subsistence on GM [gut microbiota] may overrule the host ancestry and geographic origin" (Gupta et al., 2017).

Cases like this clearly indicate that microbiome composition could be informative about socio-cultural patterns certain groups share (see also below), but not about their relatedness. Some studies have rightly taken this observation as a reason to reject the idea that race plays a role in similarities between microbiomes of different human groups. Quin and Gibson (2020) highlight "that human behavior including cultural variations in feeding practices, delivery modes and hygiene, over geography or race, are the largest predictors of microbial variability in the infant gut." In fact, "all humans have similar microbial succession during infancy." This means, if anything, 'race' is socio-culturally acquired during one's life, but not biologically inherited over lineages. Thus, this holobiont-approach to race is conceptually incompatible with standard views of human races that divide reproductive individuals into biological races, especially genetic clustering of populations.

However, we could still be pluralists about what it means to belong to a biological race, allowing individuals to be grouped in different ways as races. Instead of being reproductive individuals, holobionts could be conceptualized as physiological individuals, like developmental, immunological, or metabolic individuals (i.e. host and microbiome form a unit that develops as one, builds up one immune system, and constitutes one metabolic system), which could then be racially distinguished.

This narrative seems to underlie some microbiome relocation studies. An example is Hoffman et al. (2018)'s investigation of shifts in oral microbiota composition in the "at-risk group" of Mexican American women, their level of acculturation (e.g., English linguistic acculturation, food type acculturation), time in the US, and higher susceptibility for obesity-linked diseases. They showed that, for example, higher English linguistic acculturation is associated with an oral microbial transition from *Prevotella* to *Streptococcus* species. Thus, after acculturation, Mexican American women physiologically resemble more white US women. Based on this microbial change they predicted a shift in woman's metabolism by adapting to the US lifestyle, which could make Mexican American women more prone to obesity-related diseases. They summarized their results by stating that "the oral microbiome may prove to be one of the most informative and easily accessible biomarkers for research in low income, resource poor populations." One may understand this study as offering narratives not only about how physiologically poor bodies emerge in poor socio-economic environments and how the relocation of bodies destabilizes biological races and their health, but also about how cultural change is associated with physiological shifts from one human race to another.

This view, which identifies the holobiont as a physiological (e.g., metabolic) individual that can be grouped in different biological races, is not really a conceptual option for microbiome research, though, as it cannot escape a more general problem. Both approaches attributing race to holobionts—be they reproductive or physiological individuals—create even more fuzzy boundaries between races than genetically clustered human populations. Holobiontic units do not resemble multicellular organisms understood as bound entities delimited by their skin or clear genetic boundaries (see Skillings, 2016; Chiu and Gilbert,

2015; Baedke and Gilbert, 2020). In fact, holobionts can be seen as individuals and ecosystems simultaneously (Suárez and Stencel, 2020) and often show more affinities with multi-species communities than with individual organisms (Gilbert et al., 2012; Skillings, 2016). As a consequence, this holobiont approach to race directly leads to a number of difficult conceptual questions. For example, can ecosystems be grouped in a reasonable manner as biological races? Does it make sense to classify races without being able to individuate single organisms, but only collectives of reciprocally interwoven species?

To sum up, this second framework also leads to a conceptually problematic view of human races. It cannot make race be informative about ancestry. In addition, it struggles with identifying a clear biological unit as a particular race and with drawing meaningful boundaries between biological races. Thus, both views about how microbiota might allow distinguishing human races cannot biologically ground the concept in a convincing way.

Conclusions and outlook

We have critically assessed the recent trend in human microbiome research to classify certain social and ethnic groups as biological races with embodied traits. In this field, racial difference is conceptualized as socio-cultural difference that is inscribed into the human organism as a specific profile of microbial taxa, which affect host developmental and physiology as well as disease susceptibilities. Our analysis shows that this concept of biosocial races is in danger of slipping into novel biologizations of race, which are highly problematic, both historically and conceptually.

On the historical side, current microbial race studies reintroduce environmentalist argumentative patterns from colonial humoralism and acclimatization debates about indigeness and racial difference, in which nutrition often plays a key role. These often compare physiological, civilization, and health differences between indigenous and western populations in stereotypical ways. By extrapolating from a small number of indigenous groups as exemplars of types of bodies and civilizations, they promote a distorted view of indigenous biologies along dichotomies such as civilized–primitive, globalized–uncontacted, pure–contaminated, and healthy–ill. These findings remind us that, while we have become increasingly aware of the societal threats of race theories that draw on intrinsic (genetic) biological differences, also environmentalist views of embodied race can lead to exclusionary classifications of human biological diversity.

On the conceptual side, microbiome research faces a serious dilemma. Both conceptual frameworks available (seeing microbiomes as surrogates for human races and holobionts as races) cannot provide a consistent approach on how individuals can be grouped into races. The ‘microbiota as surrogates’-view is highly counterintuitive and taxonomically problematic. The ‘holobiont’-view decouples biological races from ancestry and evolution and cannot draw clear boundaries between biological races. Due to this dilemma, microbiome research cannot provide a convincing theoretical framework for describing biological races in humans.

We can now return to our initial question ‘Does the human microbiome tell us something about race?’ On the biological side of race, these studies cannot tell us much that is historically unproblematic or conceptually consistent. Where do we go from here? First, we strongly urge to remove the concept of race from microbial studies to describe biological properties of human groups. However, researchers may still hold that the term can be useful to grasp socio-cultural differences, i.e. the social reality of race. We are mostly skeptical about this option, too. The history of environmentalist thought has given us various examples how racial distinctions are prone to exclusionary views on indigenous cultures (and not only bodies); and there is clear evidence that

some microbiome research is already resurrecting the stereotypical and pejorative narratives (e.g., on ‘rewilding’) underlying these older views on culture.

At the same time, we acknowledge that race can, in some few contexts, be a helpful lens to critically study how social–ethnic inequalities can lead to health disparities in order to inform policies for oppressed groups, like minorities in the US (see Krieger, 2012). In short, racism is very real and could have effects on the microbiome and health. For example, Benezra (2020, p. 894) has argued that, in microbiome research, “[r]ace is meaningful as a category if the designation can be seen as an ethico-onto-epistem-ological one and not biologically a priori.” However, due to two reasons it remains unclear how this position can be generalized to non-US contexts: (i) Even though health disparities in the US can be mapped (to some degree) onto officially used racial categories, in Latin America, for example, these categories are mostly absent from administrative information and self-ascription in terms of race is less common (see Loveman, 2014; Nieves Delgado et al., 2017). Moreover, (ii) in many national contexts racial politics and racism work differently than in the US. This means that health-related inequality and discrimination processes affect different groups than those identified in US-race debates.

Second, and related to this social side of race, the usage of race as a simple proxy for complex cultural phenomena is in danger of fragmenting the social reality of microbial-mediated diseases into isolated social determinants of health (e.g. English linguistic acculturation, American vs. traditional diet). This is a general challenge of social and health disparity studies in the Global South. In face of this problem, social scientists (and some biologists) have recently requested a stronger integration of social science and humanities scholars into human microbiome research (Rees et al., 2018; Benezra, 2020; Greenhough et al., 2020). We believe such integrative efforts are strongly needed, as basically all the studies investigated by us show a strong asymmetry between the readiness to model and explain microbial complexity, but not cultural complexity. As our analysis shows, such interdisciplinary collaborations would strongly profit from not only including social scientists and anthropologists, but also historians and philosophers of science that can provide insight into the historical and conceptual dimensions of categories used. One valuable contribution of such multi-disciplinary microbiome research could be to provide new insight into how normality, health, and disease are created. Microbiome research, informed by a stronger analysis of hosts’ social, cultural, and economic situation, as well as by studies on conceptual frameworks of biological normality, boundaries, and taxonomies, can help in shifting biased views of health and avoid pathologizing certain communities.

Finally, human microbiome research is in need of stronger ethical guidelines that guarantee heavily studied groups, like the Yanomami, to be in control of the biomedical data gathered from them and to benefit from the various samples (fecal, skin, oral, vaginal, etc.) collected from their bodies. Some indigenous groups like the San and Hadza (are about to) issue their own research-ethics code that should guarantee them a greater say in research on them (Callaway, 2017). Some microbiome researchers and anthropologists have voiced support for such attempts to strengthen indigenous rights and ownership (e.g., Dominguez-Bello et al., 2016; Crittenden, 2020). We clearly agree with the need for empowering these groups. At the same time, we contend that the utilitarian stance of many of these approaches (rewarding indigenous group in some way) alone cannot justify racializing and stereotyping them. In other words, it is ethically questionable to reward these groups for being treated as a primitive microbial ‘Noah’s Ark’ that allows rewilding the western civilization (Beans, 2020).

In her review of the use of race in microbiome research Benezra (2020) states that “human microbial ecology can contribute to a more complicated view of humans.” We agree, to some degree, with this assessment. We believe that the field has a great potential and surely bears hope for addressing the biosocial nature of global health problems and the complicated link between social and health disparities in innovative new ways. But, the current state of the field, at least the part that focuses on racial differences, is rather sobering. It lacks historical awareness and strongly needs conceptual clarification. We hope scientists will take up these challenges and shift their research from tracing microbiota in reified human races towards studying microbiota in the complex social realities of hosts.

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Notes

- 1 Microbial embodiment differs from other postgenomic ways of embodiment (Krieger, 2005, Kuzawa and Sweet, 2009), which highlight socio-culturally induced changes in gene expression and physiology in human individuals. In contrast, embodied microbes, above all, extend humans' genome with possibly functionally relevant genes. It constructs a new developmental and evolutionary unit, a hologenome (a collective of host and microbial genomes; Rosenberg and Zilber-Rosenberg, 2016), above the level of human individuals.
- 2 It is common to find these two concepts used interchangeably (e.g., as 'race/ethnicity') in the microbiome literature, often without defining them. Our arguments below concern those microbiome studies that biologize ethnicity (understood as cultural diversity in human populations) or reinterpret ethnic difference as racial (biological) difference.
- 3 The idea of rewilding human microbes is informed by findings of microbial differences between lab and wild mice. This has led to attempts to breed so-called 'wildlings' (i.e. lab mice which acquired microbes of wild mice; see Rosshart et al., 2019). Another influence comes from theories of environment restoration and its potential positive effects on human's microbiome and health (see Mills et al., 2017).
- 4 While we focus on studies conducted on populations in (or from) Latin America, our arguments can be extrapolated to other geographical and national contexts. For an overview of studies, e.g., in Asia and Africa, see Gupta et al. (2017).
- 5 Genetic and genomic population studies in Latin America often use (rather inconsistently) categories like race, ethnicity, nation-belonging, and color to refer to biological differences in humans (Wade et al., 2014). We observe a similar trend in microbiome studies.
- 6 Current concepts of nutrition, environment and race differ from those during the colonial times. We use the concept of race to refer to the colonial classification system in place in which changing distinctions based on appearance, caste, origin and religion structured an unequal society in the Spanish colonies (Martínez, 2008). These 'racial' differences were not seen as fixed corporeal differences (see Earle, 2013).
- 7 Benezra (2020) calls the attempt to study and preserve disappearing microbial diversity in indigenous groups 'salvage microbiomics'. This research trend in the field includes, for example, the attempt to develop a 'Microbiota Vault' in which 'indigenous microbes' are collected and preserved that may one day be used to prevent disease (Beans, 2020).
- 8 The long research history on this group makes problematic not only how Clemente et al. (2015) frame their research object (“an isolated Yanomami Amerindian village with no documented previous contact with Western people”), but also their explanation on the presence of bacteria with functional antibiotic resistance genes in these 'uncontacted' people. In this context, one has to keep in mind that microbes travel much faster than direct human contact, e.g., through trade and soil exposure. For a detailed discussion of this study and the myth of populations' uncontactedness and purity, see Maroney (2017) and Benezra (2020).
- 9 Another taxonomic problem, which we cannot discuss in detail here, results from the lack of a consistent species concept for prokaryotes (O'Malley, 2014, ch. 3). This makes genus and phylum-level microbiota classifications prone to oversimplifications when used for distinguishing human races.
- 10 One might still argue that this view on race satisfies folk biology taxonomies. But this position would need an additional argument for why human microbiome ecology should be based on folk taxonomies.
- 11 Notice that even in those cases where microbial variation seems to be associated with populations' genetic ancestry, these associations are no indicator of the holobiont forming one reproductive unit. These associations can be due to different affinities for microbial colonialization in each new host generalization.

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Additional information

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