INTRODUCTION TO THE CONCEPT OF MICROBIOME FOR GEOGRAPHERS

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Abstract

Human microbiome is defined as the total of microorganisms inhabiting various ecological niches of human body. The enormous role of bacteria, viruses and fungi in maintaining the physiological balance of a human body lead to extensive interdisciplinary research in the field of microbiome studies. This article presents the concept of the microbiome, its impact on human health, as well as geographical and social factors that affect its shape.

Keywords: microbiome, microbiota, bacteria, Human Microbiome Project

Introduction

The microbiome is defined as "an ecological community of commensal, symbiotic, and pathogenic microorganisms that literally share our body space" [Lederberg and McCray 2001]. In the academic context, the term was first proposed in 2001 by Joshua Lederberg, Nobel Prize winner in the field of physiology or medicine from 1958. However, this is seems to be not true; the terms "microbiome" and "microbiota" were used long before 2001 [Prescott 2017]. These terms, despite some semantic similarity, are not identical. When referring to humans, "microbiota" means the microbial taxa associated with humans, while "microbiome" is the catalog of these microbes and their genes [Ursell et al. 2012]. The first documented observation of the diversity of microorganisms inhabiting the human body was made by Antonie van Leeuwenhoek (the Father of Microbiology) in 1680s. He compared his own oral and fecal microbiota and observed striking differences between the microorganisms inhabiting these two ecological niches. Similarly, the microbiota in health and disease were different [Ursell et al. 2012]. Studies on human-related microorganisms are,

therefore, as old as microbiology itself, but only the 21st century brought research techniques and methods (like 16S rDNA sequencing[1] and whole-genome sequencing[2]) that allowed such a broad and complete characterization of microbial communities.

The Human Microbiome Project was the most extensive research program aimed at understanding the human microbiome. This huge undertaking was carried out between 2008 and 2017 by the United States National Institutes of Health. The main goals of this project were as follows: (1) to take advantage of new, high-throughput technologies to characterize the human microbiome more fully by studying samples from multiple body sites from each of at least 250 "normal" volunteers; (2) to determine whether there are associations between changes in the microbiome and health/disease by studying several different medical conditions; (3) to provide both a standardized data resource and new technological approaches to enable such studies to be undertaken broadly in the scientific community [The NIH HMP Working Group 2009]. Both this project itself and many accompanying studies resulted in many discoveries; they even re-defined the status of human being. It turns out that a huge amount of our physiological abilities depends on commensal bacteria. The purpose of this article is to familiarize geographers (or generally non-biologists) with the concept of microbiome, emphasizing the impact of broadly defined geographical, social and environmental factors of its diversity.

Why shall we study microbiome?

There are various numerical data in the scientific literature concerning the question how many microorganisms inhabit human body. The most commonly reported value is 10-100 trillion, with the highest proportion of gut bacteria. Sender et Al. [2016] have made precise calculations to verify this data. In the "reference man", who weighs 70 kg, they estimated the total number of bacteria at $3.8 \cdot 10^{13}$. They also determined the total mass of these microorganisms at 0.2 kg. As a comparison, the number of human cells was estimated at $3.0 \cdot 10^{13}$. The human microbiota occupy

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[1] A technique of sequence-reading, i.e. the order of nucleotide pairs in a DNA molecule. 16S rDNA sequences are highly conserved, thus allowing the identification of microorganisms.

[2] A process of determining the complete DNA sequence of an organism's genome at a single time.

various ecological niches that differ in the availability of oxygen, pH level, connection with the external environment and many other factors, which makes it possible to talk not only about "human microbiome", but also about "gut microbiome" (which is the most recognized one), "oral microbiome", "skin microbiome", etc. Each of these microenvironments is characterized by a different set of microorganisms, in which we can distinguish core species or genera that are specific for a particular niche and nearly always found in it.

The multitude of bacteria that inhabit the human body makes us think about how they affect our lives. For some time now, there has been a trend in treating human beings not only as macroorganisms, but also as holobiont, a biological system that comprises a collection of human, bacterial, viral and fungal cells. A large number of geographical regions have been characterized in terms of microbial core species, which form a kind of microbiological signature of a human. These studies do not only have a basic dimension. The complexity of interaction between microbes and the human body, especially in the field of the immune and nervous systems, makes these microorganisms have a measurable effect on human functioning. A number of different diseases and disorders are associated with dysbiosis, which is a disturbance of the proportion between specific species of microorganisms in a biological niche. They are not always directly caused by dysbiosis.. More often it is the disturbance of metabolic pathways, which results in increased susceptibility to a disease. Examples of disorders related to dysbiosis in microbiome are presented in Figure 1.

Subsequent discoveries lead to the belief that elements of the contemporary health care system, such as personalized therapy, cannot be considered in isolation from the microbiome concept. The type and dose of a drug, time of its administration, diet during the convalescence - all of these factors are influenced by bacterial communities living mainly in the human gut. Modern epidemiology also takes into account the influence of microorganisms - the endemicity of some diseases is explained by the composition of the microbiome. The recognition of the microbiome's impact on human health has left a special mark on personalized medicine, leading to new areas of research, such as pharmacomicrobiomics.

Impact of geographical and social factors on the human microbiome

The most important factors shaping human microbiome, both on an individual and population level, include: geographical location, ethnicity, lifestyle, diet, access to

medical care and social traditions preserved in a given region. They rarely occur separately. These interactions usually take the form of a network of connections, and one factor is conditioned by another one (e.g. lifestyle is inseparable from the diet). Unfortunately, most of the available data are limited to those from the US, EU or WEIRD countries (Western, Educated, Industrialized, Rich and Democratic countries) that represent an urbanized population. It is not entirely clear what share in shaping the microbiome should be attributed to external and internal factors. It seems, however, that external factors play a much greater role than internal factors. A study carried out by Rothschild et al. [2018] on a group of over 1000 healthy individuals indicates that in the case of gut microbiome there is a significant similarity among the microbiomes of genetically unrelated individuals who share a household, but no significant similarity among microbiomes of relatives who do not have a history of household sharing. Furthermore, over 20% of the inter-person microbiome variability is associated with factors related to diet, drugs and anthropometric measurements. Another study shows that the degree of microbial similarity in monozygotic and dizygotic twins is almost identical [Turnbaugh et al. 2009].

Diet

Among the environmental factors mentioned above, the diet appears to be the most important element shaping the microbiome (especially gut microbiome). In general, among the taxa present in the intestine we can observe two main genera of bacteria that can be treated as the biomarkers of diet: Bacteroides and Prevotella [Gorvitovskaia et al. 2016]. The predominance of Bacteroides in the gut microbiota is observed in Western urban industrialized population and is associated with high consumption of processed high-fat and high-protein food. Prevotella, on the other hand, predominates in the case of traditional, plant-based diets (e.g., traditional diets in rural communities of Africa), rich in complex carbohydrates [Ursell et al. 2012]. The proportion between these two bacteria has a tangible impact on a host health. A study revealed that high Prevotella/Bacteroides ratio makes subject more susceptible to lose body fat on diets high in fiber and whole grain than subjects with a low Prevotella/Bacteroides ratio [Hjorth et al. 2018]. According to a study conducted on Prevotella, this bacterium is linked to chronic inflammatory conditions. Using mouse model, it was observed that Prevotella is associated with systemic white cells activation and led to worse prognosis in arthritis and HIV infection [Ley 2016]. The gut microbiota is related even to mental health (gut-brain axis). High abundance of Bacteroides was correlated with an increased risk of depression [Evrensel and Ceylan 2015].
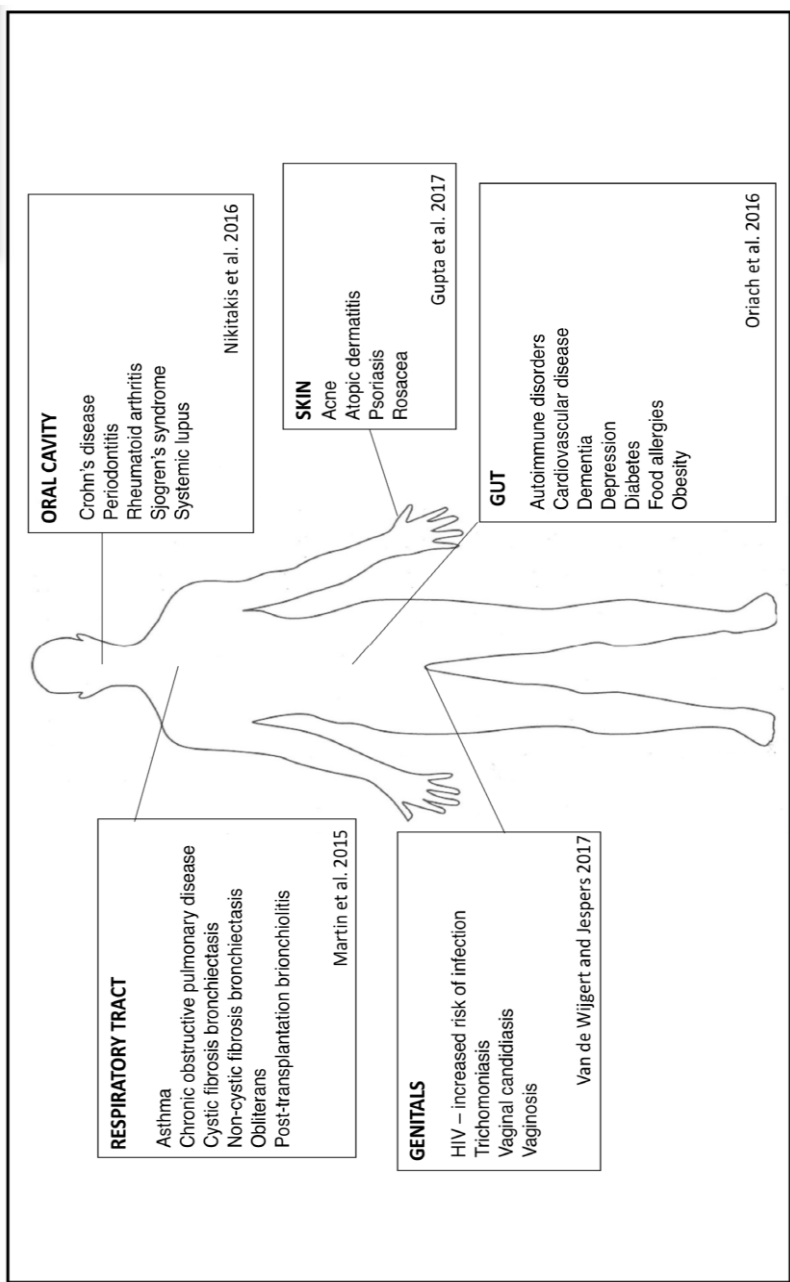
Fig. 1. Diseases and disorders caused by dysbiosis in various human microbiomes

Several studies have been conducted in order to determine the link between the diet and microbiota. Comparison of gut microbiota of Native Africans and African Americans revealed dominance of Prevotella (and other butyrate-producing bacteria) among Native Africans, whereas Bacteroides was characteristic for American Africans. It was attributed to the higher intake of animal proteins, fat and low intake of fiber by the latter. The diets of these two groups are fundamentally different from the perspective of preparation, cooking and composition. Animal fat and protein consumption was 2-3 times higher among African Americans, while carbohydrate and fiber intake, mainly in the form of resistant starch, was higher among Native Africans. Apart from various composition of gut microbiota, an increased risk of colon cancer (which is a typical "westernized" disease) was observed among Americans. It is known that the products of fiber fermentation conducted by Prevotella possess anti-inflammatory and anti-cancerous properties and that the products of bacterial bile acid conjugation are of carcinogenic character. Obtained results suggests two potential mechanisms for diet-associated cancer risk: the protective effect of dietary fiber and the promotional effect of dietary fat on stimulating bile acid synthesis by the liver [O'Keefe et al. 2015]. Another study focused on differences between gut microbiota of children from Burkina Faso on the one hand and from European countries on the other hand. The obtained data indicate an association between polysaccharide-degrading microbiota and the calories that the hosts can intake from their diet, which can potentially influence the survival and fitness of the host. Furthermore, a higher microbial richness and biodiversity were observed among children from Africa. This fact has beneficial consequences: short-chain fatty acids-producing bacteria that are abundant among African children possibly help prevent the establishment of some potentially pathogenic intestinal microbes causing diarrhea [De Filippo et al. 2010].

The influence of a diet on microbiota was also confirmed, to some extent, in an oral microbiome. A study revealed that the consumption of saturated fatty acids and vitamin C was consistently correlated with alpha (within sample) microbial diversity indexes in both richness and diversity. The intake of saturated fatty acids was also correlated with relative abundance of fusobacteria, which are involved in many human infections that cause tissue necrosis[3] and septicaemia[4]. It seems, however, that

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[3] A sequence of morphological changes occurring after cell death in a living organism.
[4] A life-threatening organ dysfunction caused by disturbed regulation of the body's response to infection.

the diet does not have as much effect on oral microbiota as in the case of the gut microbiota [Kato et al. 2017].

Ethnicity

Several studies consider ethnicity as a significant factor that affects human microbiome. A study compared the oral microbiome composition in the samples obtained from major races/ethnic groups residing in the United States (African Americans, Caucasians, Asians and Latin Americans). It was found that nearly 50% of the overall bacteria genera significantly differ in abundance between the above-mentioned populations [Mason et al. 2013]. Since in this case both groups African Americans and Caucasians were subjected to similar environmental factors like food, nutrition and lifestyle, it is suggested that the difference in the anatomical structure of teeth results in distinct composition of oral microbiome [Gupta et al. 2017]. A comparison of the vaginal microbiota in healthy Caucasian and African American women from North America showed that the microbial communities of the first group are dominated by bacteria of the genus Lactobacillus, while in the latter the most represented genus was Atopobium [Zhou et al. 2007]. This variance has a significant impact on the different susceptibility to reproductive system diseases. Lactobacillus genus belongs to the ecological group of lactic acid bacteria, which are considered to play a beneficial role in human health. On the other hand, elicited level of Atopobium is regarded as a signature of significant disruption of immune barrier properties, potentially resulting in enhanced susceptibility to sexually transmitted infections during bacterial vaginosis [Doerflinger et al. 2014]. Zhou et al. [2007] hypothesized that host genetics (mainly connected to the innate and adaptive immune system) may be more important in shaping the vaginal microbiome than the cultural differences between ethnic groups.

Another comparative study demonstrated a stratification of gut microbial composition in Malaysian pre-adolescents. The Malays, Chinese and indigenous Orang Asli were subjects of this research. The highest microbial diversity was found in the economically deprived indigenous children while the lowest diversity was detected among relatively wealthy Chinese children. It is suggested that a combination of low income and low parental education attainment might have resulted in reduced hygiene practices among Orang Asli children in comparison to Malays and Chinese children. In addition, it was found that the pathways pertinent to bacterial colonization and chemotaxis are over-represented in Orang Asli population, whereas pathways related to sugar metabolism are higher in the Chinese population [Chong et al. 2015].

The aim of the research conducted among two groups of Canadian infants – Caucasians and South Asians – was to investigate whether the infant gut microbiota differed by ethnicity and by breastfeeding status. It was found that several members of the lactic acid bacteria group were more abundant within South Asians. These bacteria are known to break down carbohydrates that are not absorbed by the host to produce acetate and lactate, which are used as energy sources by other microbes. This observation is linked with a higher rate of vegetarianism among South Asian mothers and with a higher breastfeeding rate. Authors also demonstrated other factors that underlie the construct of ethnicity used in this study: vegetarian status, gestational diabetes mellitus prevalence, timing of introduction of solid foods, antibiotic use during pregnancy, mode of delivery, etc. [Stearns et al. 2017].

Lifestyle

The impact of lifestyle on human microbiome is noticeable at both individual and population levels. Some authors have suggested that the type of delivery (vaginal or caesarean) influences the composition of infant's microbiota. It was also suggested that breastfeeding (or its absence) do so as well [Pannaraj et al. 2017]. For example, Dominguez-Bello et al. [2010] demonstrated that the skin, oral mucosa and nasopharynx of neonates vaginally born were colonized predominantly by Lactobacillus, whereas babies delivered by caesarean section were colonized by a variety of potentially pathogenic bacteria typically found on the skin and in hospitals (Staphylococcus and Acinetobacter), suggesting that babies born by caesarean delivery were rather colonized with skin microbiota than with vaginal type of bacteria. It was also shown that caesarean delivery may disrupt the gut microbiome of newborns for up to 6 months after birth [Grölund et al. 1999]. A study concerning the role of breastfeeding in shaping microbiome found that nearly 30% of the beneficial bacteria in a baby's intestinal tract come directly from mother's milk, and additional 10% come from the skin on the mother's breast [Pia et al. 2017].

At the population level, an investigation of the phylogenetic diversity and metabolite production of the gut microbiota from a community of human hunter-gatherers, the Hadza of Tanzania, showed an interesting relationship attributed to the broadly understood lifestyle. Compared to Italian urban controls, the Hadza are characterized by higher levels of microbial richness and biodiversity. The Hadza gut microbiome possess characteristic features that are consistent with a heavily plant-based diet (e.g, the predominance of Prevotella). Another finding in this study is a sex-related divergence in Hadza gut microbiome structure, which is not documented in other human

groups. This divergence is believed to be based on the Hadza sexual division of labor and differences in diet composition among female and male individuals. Although inhabiting the same environment and feeding on the same food, both groups of population have adapted to available resources in a different way [Schnorr et al. 2014].

Another study, conducted in seven villages in Southwest Cameroon, highlighted the role of a parasitic infection (amoebiasis) in the shaping of gut microbiome. The study revealed that individuals harboring amoeba exhibit significantly higher alpha diversity (within sample) in their gut microbiota, coupled with a significant reduction in beta diversity (between samples). This phenomenon could be explained by either direct or indirect interactions between gut microbiota, amoeba and host immune system. It has been hypothesized that the underlying cause of the high incidence of autoimmune diseases, characteristic for industrialized countries, is the absence of childhood exposure to infectious agents, such as parasites. More diverse microbial communities are considered to be beneficial due to lesser susceptibility to perturbations [Morton et al. 2015]. In the same study, the authors compared the gut microbiota composition of people from the same subsistence mode and genetic ancestry. It was found that the differences exist within the group of hunter-gatherers and they cannot be attributed to diet or parasitism. This finding suggests an important role of other, unexplored and very localized environmental factors (e.g. different water sources). Key differences were found among hunter-gatherers and fishing or farming populations. They probably reflect the influence of a long-term diet, which depends on a lifestyle [Morton et al. 2015].

Also, the variation in skin microbiome was attributed to a different lifestyle and environmental conditions. A comparative study conducted among the US and Tanzanian populations revealed that the bacterial communities found in the US hand-wash samples consisted of "typical" skin-related bacteria species, while the most abundant taxa found among Tanzanians included environment-associated microorganisms that are not believed to be typical colonizers of human skin. They are, however, commonly found in soil and aquatic environments. Notable lifestyle differences between the US and Tanzanian participants have been identified. US participants spend the majority of time indoors in contact with dry surfaces and none of the US study participants was a caregiver for young children. By comparison, mothers from the Tanzanian population who took part in the study lived in open-air residences and were typically outdoors when performing daily household activities that require al-

most constant contact with soil, untreated water and other outdoor surfaces [Hospodsky et al. 2014].

In terms of a lifestyle, a special attention has been paid to so-called "built environment microbiome". This term has been formed on the basis of observations that every type of a building possesses its own microbiome. Humans, pets, plants, plumbing systems, heating, ventilation and air-conditioning systems, mold, dust resuspension and the outdoor environment have been identified as the major sources of airborne bacteria that inhabit built environment [Prussin and Marr 2015]. Differences in the built environment microbiome composition have been linked to an increased risk of allergy and asthma [Casas et al. 2016]. It is also assumed that variations in this microenvironment may be responsible for mental health problems [Hoisington et al. 2015].

Conclusions

The examples presented above constitute only a small part of the research on the microbiome-geography relationship. In the recent years, this topic has been widely discussed, and thus, it has been explored by a number of research groups around the world. It seems that the concept of the microbiome itself, as well as the techniques used in the studies devoted to it, present themselves as a very promising tool in the hands of geographers of all (or almost all) specialties. Studies on the microbiome can shed new light on the difficulties faced in descriptive epidemiology, public health, tropical medicine and other fields related to medical geography. Agricultural geographers may be interested in the analysis of microbial communities in plants of economic importance. This is particularly useful for plants the usefulness of which is inextricably linked to bacteria, such as common grape vine. Knowledge about the species of bacteria living in or on the plant can improve the processes leading to increased yields and provide plants with adequate protection. Biogeographers may consider microbiome as a convenient tool that can help in the analysis of the history of animal migration, the composition of their diet, and the mutual relationships between particular species. Specialists in the field of land management can study microbiota to investigate the interaction between individual landscape elements. Built environment microbiome may be an object of interest for urban geographers. The use of bacteria in a geographical research seems to have almost no limits. The gradual reduction in costs of techniques used to analyze bacterial communities (e.g., the aforementioned sequencing) can be an incentive for undertaking such interdisciplinary research.

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WPROWADZENIE DO KONCEPCJI MIKROBIOMU DLA GEOGRAFÓW

Streszczenie

Mikrobiom ludzki definiowany jest jako ogół mikroorganizmów zamieszkujący różne nisze ekologiczne naszego organizmu. Ogromna rola, jaką pełnią bakterie, wirusy i grzyby w zapewnianiu wewnętrznej równowagi fizjologicznej sprawiła, że w ostatnich latach obserwu-

je się bardzo duże zainteresowanie badaniami nad mikrobiomem. Niniejszy artykuł prezentuje koncepcję mikrobiomu, jego wpływ na zdrowie człowieka, a także czynniki geograficzne i społeczne, które kształtują ludzką mikroflorę.

Słowa kluczowe: mikrobiom, mikrobiota, bakterie, Human Microbiome Project