

Mainstreaming Microbes across Biomes

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Bacteria, fungi, and other microorganisms in the environment (i.e., environmental microbiomes) provide vital ecosystem services and affect human health. Despite their importance, public awareness of environmental microbiomes has lagged behind that of human microbiomes. A key problem has been a scarcity of research demonstrating the microbial connections across environmental biomes (e.g., marine, soil) and between environmental and human microbiomes. We show in the present article, through analyses of almost 10,000 microbiome papers and three global data sets, that there are significant taxonomic similarities in microbial communities across biomes, but very little cross-biome research exists. This disconnect may be hindering advances in microbiome knowledge and translation. In this article, we highlight current and potential applications of environmental microbiome research and the benefits of an interdisciplinary, cross-biome approach. Microbiome scientists need to engage with each other, government, industry, and the public to ensure that research and applications proceed ethically, maximizing the potential benefits to society.

Keywords: microbiology, environmental science, human ecology, aquatic ecosystems, soil science

There are seemingly daily revelations about the influence that microbial communities have on human health. Such revelations have generated significant public interest in the human microbiome, highlighted by the rise of products such as gut health cookbooks, probiotic supplements, microbially enhanced yogurts, and the revival of fermented foodstuffs, such as kombucha. There is growing awareness that humans are walking ecosystems, dependent on the microbial communities living in and on our bodies.

Although public interest in the human microbiome has flourished, the awareness of environmental microbiomes—including ambient marine, freshwater, aerial, and terrestrial microbiomes—and their importance has not. Environmental microbiology has played a key role in the history and development of microbiome technology. Most clinically relevant antibiotics were isolated from soil microbes, and the majority of antimicrobial resistance genes may have originated from environmental bacteria (Cantas et al. 2013). Similarly, the first shotgun metagenomes and single-cell genomes were sequenced from marine microbes (Breitbart et al. 2002; Zhang et al. 2006). Environmental microbiomes are at the heart of nutrient cycling in both aquatic and terrestrial environments; provide essential ecosystem services, such as carbon dioxide drawdown and oxygen production, with

a central role in determining the impact of climate change (Cavicchioli et al. 2019); and are intimately linked to human microbiomes and health (Hanski et al. 2012; Stein et al. 2016). A greater awareness of the importance of environmental microbial communities is therefore critical from both ecological and human health perspectives.

In this article, we highlight the value of environmental microbiome science by describing current and potential future applications. We use global microbial data sets to explore how microbial communities are shared across human, terrestrial, and aquatic environments. We then analyze microbiome citation trends across disciplines to investigate the degree of interdisciplinarity between human and environmental microbiome research. We conclude by raising key challenges in advancing interdisciplinary microbiome science, including the emerging ethical complexities and engaging the public in the debates at the center of shared human–environment microbiome science.

Applications of environmental microbiome science

Environmental microbiome research has an extraordinary range of applications (figure 1). Early applications of environmental microbiome science included monitoring the safety of food and water supplies, and this remains an

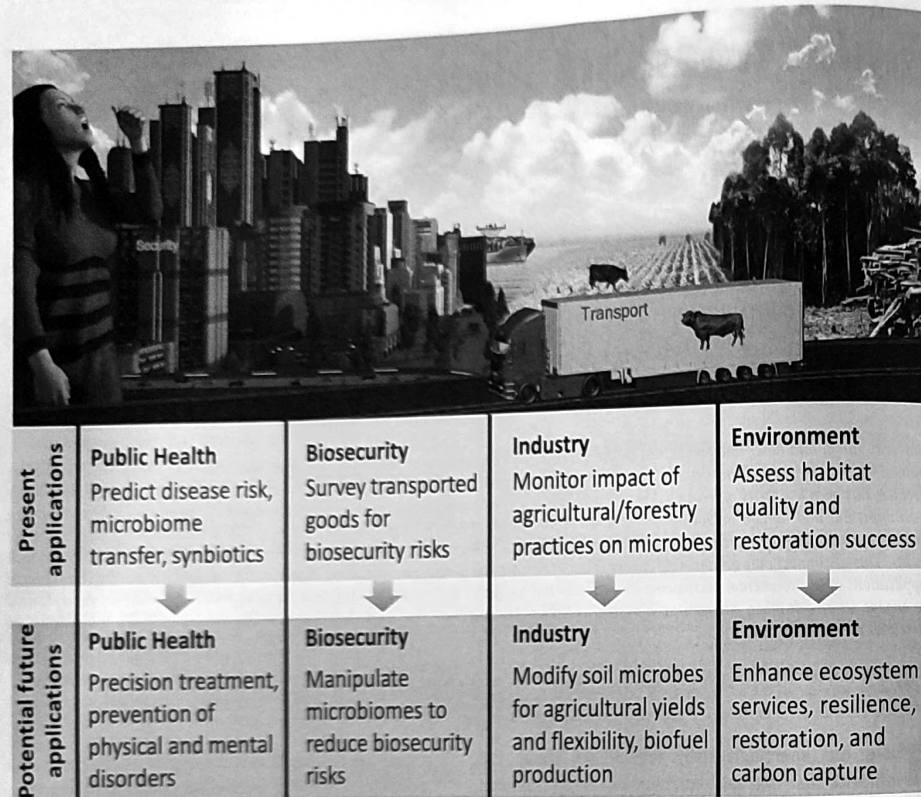


Figure 1. The applications of microbiome science span all environments and all facets of society. This figure depicts some current and possible future applications for public health, biosecurity, industry, and the environment. Potential future applications can best be realized with greater cross talk among scientific fields.

important function today. More recently, applications in areas such as agriculture, biosecurity, environmental impact assessment, and ecological restoration have vastly expanded, boosted by developments in high-throughput DNA sequencing that allow us to rapidly characterize microbial communities. Specific examples include using microbiome science to detect plant pathogens in terrestrial ecosystems (Tremblay et al. 2018), identify harmful microalgal taxa in ship ballast and marine port sediments (Shaw et al. 2019), and assess the impact of aquaculture on benthic communities (Pawłowski et al. 2014). Microbiomes have been validated as an indicator of ecosystem health: in terrestrial environments, soil bacterial communities match stages of ecological restoration (Liddicoat et al. 2019), and microbial communities can indicate the ecological condition of an estuary (Chariton et al. 2015, Raes et al. 2020).

Future applications of environmental microbiome research are certain to expand with developments in microbiome engineering—that is, actively altering microbial communities to achieve desired outcomes. Microbiome engineering for health outcomes is already apparent in

the widespread availability of pre-, pro-, and synbiotics for human use. In an environmental microbiome context, indirect microbiome engineering has been used to improve wastewater treatment (Barnard et al. 2017), whereas agricultural scientists have begun to use microbiome engineering to improve plant resilience to disease and other environmental stresses (Berg and Koskella 2018, Qin et al. 2016) and manipulate key traits such as flowering time (Panke-Buisse et al. 2015).

With further development, there is the potential for much broader applications of microbiome engineering—for example, inoculating soils or seeds to improve restoration outcomes (Muñoz-Rojas et al. 2018, Wubs et al. 2016), engineering coral microbiomes to enhance their resilience to climate change (Epstein et al. 2019), and modifying urban environmental microbiomes for human health outcomes (Flies et al. 2017, Mills et al. 2017, Watkins et al. 2020). The pinnacle of microbiome engineering may be creating synthetic microbial communities (Großkopf and Soyer 2014), which have already been developed for biotechnology applications such as biofuel production (Minty et al. 2013).

Biome

■ Ocean
■ Soil
■ Human

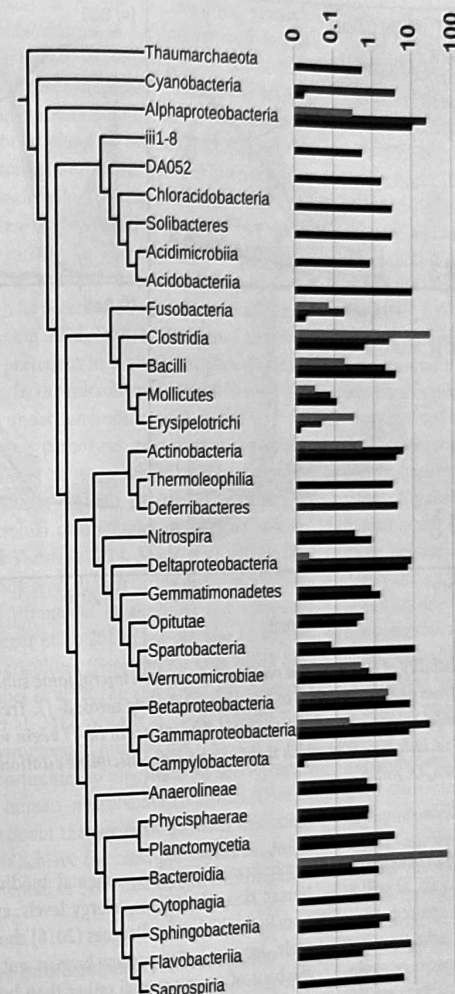


Figure 2. The shared taxonomy among ocean, soil, and human microbiomes. The plot shows the relative abundance of bacterial classes based on three large bacterial 16S ribosomal rDNA data sets representing marine, soil, and human microbiomes (Human Microbiome Project Consortium 2012, Earth Microbiome Project, Thompson et al. 2017, International Census of Marine Microbes, Zinger et al. 2011). Some taxa were largely restricted to a single biome (e.g., *Spartobacteria* and *Acidobacteriia* for soil, *Deferribacteres* and *Cyanobacteria* for oceans). However, all taxa detected in the human microbiome are also present in both the soil and ocean microbiome. A more holistic understanding of microbial communities is required to better understand, conserve, restore, and control microbial community function.

The enormous potential of environmental microbiome science to support ecological and social outcomes is therefore clear. However, if we are to harness environmental microbiome research—particularly environmental microbiome engineering—safely, and to fulfill its potential, we must ensure a solid understanding of cross-biome interactions.

Unless we know how microbes are shared across individuals, species, and ecosystems and how environmental and human microbiomes interact, we cannot best apply microbiome science for human and ecological benefit, nor can we know the potential repercussions of such microbiome manipulations.

Biomes share microbes

To demonstrate the interdependence of biomes and microbiomes, we compared the class and genus-level taxonomic composition of three large bacterial 16S ribosomal DNA data sets representing marine, soil, and human microbiomes (Human Microbiome Project Consortium 2012, Earth Microbiome Project, Thompson et al. 2017; International Census of Marine Microbes, Zinger et al. 2011; see the supplemental material for methods). The combined data set contained more than 4000 samples and over 330 million reads. Thirty-four classes of bacteria were abundant (more than 1% relative abundance) in ocean, soil or human microbiomes; of these taxa, 67.6% were shared across two or more biomes, showing the microbial connectedness of these seemingly disparate environments (figure 2). Studies examining the forces shaping the human microbiome have underlined this point, demonstrating that environmental microbes influence human microbiomes and affect our health (Hanski et al. 2012, Rothschild et al. 2018, Stein et al. 2016). Research into the cross-biome comparative function and ecology of these bacterial taxa would advance both human and environmental microbiome science.

Only a few taxonomic classes in this analysis were restricted to a single biome (e.g., *Spartobacteria* and *Acidobacteriia* for soil, *Deferribacteres* and *Cyanobacteria* for oceans). Interestingly, although the human microbiome data set was much less diverse at the class level than the soil or marine data sets (three classes

with more than 1% relative abundance, compared with 21 and 14 classes in the soil and marine data sets, respectively; figure 2), all classes abundant in humans—*Bacteroidia*, *Deferribacteres*, and *Clostridia*—were shared with both marine and soil biomes. At a finer taxonomic level, we found 72 genera were detected in all three biomes (supplemental

2019). There is also some argument over important experimental and analytical steps, such as whether to rarefy data to control for the number of DNA sequences obtained per sample (McMurdie and Holmes 2014, Weiss et al. 2017), although several best-practice guides have recently been published (e.g., Eisenhofer et al. 2019, Knight et al. 2018, Zinger et al. 2019).

Mainstreaming environmental microbiomes

Clearly, environmental microbiome science has much to offer a world grappling with fundamental environmental and human health challenges. However, some key questions remain: What must we do to help mainstream environmental microbiome science into sectors as diverse as biosecurity, urban planning, agriculture, and human health and across a diversity of countries and cultures? How can we best support well-informed decisions and ensure applications are grounded in a well-developed understanding of the opportunities, uncertainties and risks? How can we ensure that the benefits of microbiome science are not limited to the rich but address challenges faced by all people and are integrated into policy and practice to address some of the world's most serious human and environmental challenges?

As well as collaborating across disciplines, microbiome science will benefit from engaging with practitioners, policymakers, regulators, and a diverse range of human communities to achieve the greatest possible impact. Human microbiome science provides the best examples to date of achieving this engagement, helping to explain the growing public awareness of this field and the comparative lag in environmental microbiome science. The American Gut Project (<http://humanfoodproject.com/ameriCangut>) exemplifies successful public engagement, having crowd-sourced funding and samples from over 11,000 participants from more than 40 countries (McDonald et al. 2018). Microbiome science is now available to the general public via print and electronic media in popular science TV shows, TED talks, podcasts, and books, many of which are presented or authored by leading scientists in the field. Greater collaboration between scientists and the media also reduces the potential for sensationalized science reporting, which would facilitate communication, understanding, and trust between the public and microbiome researchers.

Projects such as the Healthy Urban Microbiome Initiative (www.HUMIglobal.org) that integrate the natural, social, and health sciences show the potential for international, transdisciplinary collaboration, but how can we encourage more transdisciplinary microbiome science collaboration? There are well-known barriers to transdisciplinary activity in any field (Rogers 2010), ranging from tension over appropriate methods of inquiry to differences in lexicon and communication practices used by scientists within disciplines. A unified microbiome vocabulary has been proposed that may help overcome these barriers and reduce misunderstandings among both the scientific

and broader community (Marchesi and Ravel 2015). An emphasis on accessible data and analysis code, as well as minimum metadata standards (<http://gensc.org/mixs>), help facilitate connectivity and reproducible science—all of which we strongly encourage. Bacterial and archaeal full-length 16S ribosomal RNA gene reference sequence databases are biased toward host-associated organisms, with less than 25% of sequences originating from soil or aquatic environments (Schloss et al. 2016). Integrating future sequencing efforts with multi-omic data storage options for both sequences and metadata will make connecting across biomes easier. For example, expanding the Human Microbiome Project repository to include environmental data from both soil and ocean biomes is likely to foster cross-discipline connections (Tasnim et al. 2017). Furthermore, multi-agency funding to develop broadly applicable tools can help reduce redundancy and facilitate cross-biome comparisons (Alivisatos et al. 2015).

Conclusions

Microbiome science is shifting the social perception of microbes from disease causing, unhygienic organisms to potential partners vital for human and ecosystem health (Cavicholi et al. 2019). Scientists now recognize the importance of microorganisms for ecosystem function. However, our understanding of the contributions made by microbes within a system and how they are shared and interact across ecosystems and biomes is incomplete, hindering our ability to translate microbiome science into safe applications for the greatest environmental and human health impact.

We are not the first to suggest that a coordinated, intensely collaborative research effort is needed to fill these gaps. For example, the interdisciplinary Unified Microbiome Initiative was proposed to develop cross-cutting microbiome technologies in order to facilitate translation into applications (Alivisatos et al. 2015). Furthermore, we should co-develop research with environmental and health practitioners and work across disciplines to understand how microbiome technology can be safely applied. We must be ready to help national and international watchdogs grapple with novel regulatory challenges and support policymakers to breach silos and build bridges between traditionally disparate sectors. It is highly important that we also engage the public with integrity, clarity and skill to maintain public trust and support the development of a microbiome-literate community (Shamirina et al. 2017)—taking heed, as well as we can, of the lessons from climate change science communication (Bostrom et al. 2013). Microbiome research and discourse should include people from a range of national, cultural, genetic and socioeconomic backgrounds to ensure the applications are distributed equitably. These are no small challenges, but ones that we must overcome to ensure that we are collectively equipped to develop, understand and translate microbiome science for maximal global benefit.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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