Environmentality in biomedicine: microbiome research and the perspectival body

Joana Formosinho*, Adam Bencard, Louise Whiteley

Medical Museion, Department of Public Health and Novo Nordisk Foundation Center for Basic Metabolic Research (CBMR), University of Copenhagen, Denmark

ARTICLE INFO

Keywords:
Microbiome
Environment
Public health
Holobiont
Biomedicine
Situated knowledges

ABSTRACT

Microbiome research shows that human health is foundationally intertwined with the ecology of microbial communities living on and in our bodies. This challenges the categorical separation of organisms from environments that has been central to biomedicine, and questions the boundaries between them. Biomedicine is left with an empirical problem: how to understand causal pathways between host health, microbiota and environment? We propose a conceptual tool – environmentality – to think through this problem. Environmentality is the state or quality of being an environment for something else in a particular context: a fully perspectival proposition. Its power lies partly in what Isabelle Stengers has called the efficacy of the word itself, contrasting the dominant sense of the word environment as something both external and fixed. Through three case studies, we argue that environmentality can help think about the causality of microbiota vis-a-vis host health in a processual, relational and situated manner, across scales and temporalities. We situate this intervention within historical trajectories of thought in biomedicine, focusing on the challenge microbiome research poses to an aperspectival body. We argue that addressing entanglements between microbial and human lives requires that the environment is brought into the clinic, thus shortening the conceptual gap between medicine and public health.

1. Introduction

In this paper, we argue that the prominence of microbiome research in the 21st century is bringing about changes in the status of the environment within biomedicine. Categorical distinctions between organisms and environments are brought into question, and the biological boundaries between them become less clear. We argue that this introduces challenges regarding usage of the term environment: what constitutes an environment, for whom, and with which consequences for health? We situate microbiome research historically within medical and biomedical currents of thought from the 19th century onwards, particularly vis-a-vis the rise to dominance of a place neutral medicine. We then offer a conceptual response to the challenge of proliferating environments in microbiome research.

The word microbiome refers to the combined genetic composition of the microbiota—bacteria, viruses, archaea and fungi—that live on and in the body of another organism (a host, e.g., a human). Microbiome composition is different from individual to individual, seems to impact host health and wellbeing in far-reaching ways, and changes over the lifespan of the host according to myriad factors such as diet, social interactions, place and antibiotic intake (e.g., Lynch & Pedersen, 2016). This complex collection of microscopic organisms is frequently described as an inner environment or ecosystem (Nerlich & Hellsten, 2009) in metabolic dialogue with the environment outside. It has also been described as a functional component of the macro-organism, with microbiota and host making an integrated unit called the holobiont.1 Through either lens, microbiome research brings organisms and environment closer: they are co-constituting over time, and across scales from macro to micro.

Whether and when microbiota-host relations should be framed in ecosystemic terms or as part of an integrated unit of individuality is a matter of ongoing debate. Diverse attempts have been made to delineate levels of integration—for example, evolutionary, developmental, physiological, immunological—and the consequences for individuality.

* Corresponding author. Medical Museion, Fredericiagade 18, 1310 Copenhagen K, Denmark.
E-mail address: joana.formosinho@sund.ku.dk (J. Formosinho).

1 The concept of holobiont is most often traced back to Lynn Margulis (1991, sometimes 1990) to describe the unit comprised of a host plus its primary symbiont (see Baedke et al., 2020; and Saizán, 2018, for longer historical lineages). The term is now used more broadly to describe the unit comprising a host and its community of symbionts (e.g., Gilbert et al., 2012). A related concept of ‘metaorganism’ (Bosch & McFall-Ngai, 2011) highlights the synergistic interdependence between host and microbiota.

https://doi.org/10.1016/j.shpsa.2021.11.005
Received 2 March 2021; Received in revised form 18 October 2021

0039-3681/© 2021 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).
Arguments have been made that host and microbiota are integrated biological individuals, the aforementioned holobionts (e.g., Gilbert et al., 2012; Gilbert & Tauber, 2016; McFall-Ngai, 2013; Theis et al., 2016); that holobionts are constitutively embedded in their world but not biological individuals (Smith, 2017); that host and organisms are ecological communities without unity (e.g., Douglas & Werren, 2016; Moran & Sloan, 2015; Skillings, 2016; Stencel & Proszewska, 2018), and that holobionts are individuals construed as processes of intersecting lineages collaboratively in metabolism (Dupr et al., 2009). Suarez and Stencel (2020) have argued that both ecosystemic and integrated individuality perspectives can hold, depending on whether we adopt the perspective of the host or the microbiota; Dupré (2012) has argued that boundary demarcation should be decided in context depending on biologically salient aspects of the analysis. Within biology, the two perspectives are not generally considered incompatible (e.g., see Gilbert, 2019).

A kind of ontological fracturing is thus taking place (Landecker, 2019). Categories such as individual/community, organism/environment, inside/outside, are creaking under the weight of experimental data (Landecker, 2019). Whilst not dissolving completely, categories begin to leak into one another, with epistemic and ontological consequences that invite re-thinking the kinds of questions we ask in biology and biomedicine; the modes of intervention we consider; and the worldviews that underly them. Landecker and Kelty’s (2019) invitation to think metabolic disorder through short-chain fatty acids produced at the metabolic interface between microbiota and host—rather than thinking through genes or calories—is one example of such thinking reversals. Faecal microbiota transplantation (see section 3) is an example of a shift towards ecosystemic modes of thinking within medical intervention; another is the development of probiotic based cleansing products for use in hospitals (see Caselli & Purificato, 2020).

Many have argued that shifts in imagery and metaphor indicate (and follow) shifts of thought in science (Haraway, 2004; Keller, 2020). Indeed, ecosystemic imagery and metaphors have been a core driver of scientific articulations of the importance of microbiome research, as well as its uptake in public and media discourses (Sangodoyi, 2014). McFall-Ngai et al. (2013, p. 3233) write of the holobiont as “the ecosystem that is an individual animal and its many microbial communities.” Gilbert (2019, p. 308) similarly writes that “we are not only organisms, we are biomes—sets of integrated ecosystems”, and Gilbert et al. (2012, p. 336) write that “we are all lichens.” This richness of imagery and metaphor has been coupled with widespread societal attention to the implications of thinking with and through microbial environments. Popular books and journal articles alike draw on cultural touchpoints such as Walt Whitman’s I contain multitudes (e.g., Podolsky, 2012; Yong, 2017) and sci fi tropes such as We are not alone (e.g., Shivaji, 2017; YourekaScience, 2014), to indicate disturbance to notions of the sovereign individual.

Responding to this landscape of categorical frictions and fractures as interdisciplin ary scholars,4 our paper proceeds in three sections. In section 2, we lay out the historical landscape: situating the microbiome projects as the successors and intellectual disruptors of the human genome project, and arguing that clinical microbiome research sits uncomfortably within the prevailing paradigm of place neutral medicine. We argue that this research is changing attention to environmental factors within human health. Notably and importantly for our argument, we argue that microbiome research troubles notions of what actually constitutes an environment, and for whom.

In section 3 of the paper, we propose a conceptual response to the challenges of proliferating usages of environment in microbiome research. This is environmentality,5 which we define as the locally described state or quality of being a causal context for something else. Environmentality has a dual action as concept and as term; that is to say, its value lies partly in contributing to conceptual debate about what constitutes environment, and partly in the action of the word itself. It is a tool for sharpening attention to what may count as an environmental factor in localised and case-specific ways, over time and across scales, from micro to macro. And it is also a way of highlighting cultural meanings imbued in the word environment—namely a gravity towards the external, the adjacent and the fixed—which may be influencing ability to respond to epistemological and ontological challenges posed by a microbial view. We illustrate how environmentality has shaped our thinking through three case studies. Sections 2 and 3 should be read as in dialogue with each other. They speak in different voices, and section 3 is a conceptual response to a problem laid out in section 2.

2 Environmentality has also been used as a play on Foucault’s governmentality, applying it to the area of environmental governance (Luke, 2011; Agrawal, 2005; Jepson, Bramstrom, & Persons, 2012). There have also been usages of the term in literary theory and ecocriticism (e.g., Bartosch, 2013; Azzarello, 2012). These are different usages to the one we provide here, and we don’t address them directly.

2 See Morar and Bohannan (2019) for an analysis of the different metaphors and framings used to think through microbiome research.

3 As a team, we employ tools from STS, HPS, history and medical humanities.
or singular pathological entities, towards the study of microbes as ecologies and communities (Paxson & Helmreich, 2014). Growing concern in the 1990s about the rapid spread of antibiotic resistant microorganisms as a major health threat was a key factor in this shift; see Landecker (2016) and Sariola and Gilbert (2020) on changing biologies of bacteria in a world of human desires, and ensuing changes to human ideas of the bacterial. Joshua Lederberg wrote in 2000 (p. 290) that a re-conceptualization of disease as “instabilities within this context of cohabitation” was imperative. Highlighting environmental co-existence with microbes was thus not only a rhetorical device used to further an exciting and undereported research area, but was also a substantive response to the growing realization of the depth and complexity of the entanglement between human and microbe. From this perspective, disease in general had to be understood as an environmental phenomenon, or at least as always having environmental qualities.

The newness of this ecological vision for biomedicine must be appreciated in historical context; it stood in stark contrast to the genomic science it was built upon. As Nerlich and Hiilsten (2009) have described, post-genomic microbiome research cast itself and its objectives in a very different register than the linguistic metaphors that had dominated the Human Genome Project (HGP). Where the HGP had been presented as a deciphering of the book of life, with the genomic sequence as constructed from letters (bases) and chapters (chromosomes) organised in books (genomes), microbiome research deployed a language of interactions, communities and ecologies (Baty et al., 2014). The genomic vision of the late 20th century was one in which the mysteries of the human organism would be mostly solved by looking within, deeper and deeper into the molecular information contained in its cells (Keller, 2000). Geneticist Walter Gilbert in 1992 summarised this view and its belief in the revolutionary promises of the Human Genome Project by stating that one day “three billion bases of DNA sequence can be put on a single compact disc and one will be able to pull a CD out of one’s pocket and say, ‘Here is a human being; it’s me!’” His essay was entitled A Vision of the Grail, and was published in a book called The Code of Codes (Kevles and Hood, 2000 (p.96).

Unlike the relatively bounded metaphors of organisms as books, the rise of microbiome research was part of dragging the human organism into what Paxson and Helmreich (2014, p. 166) describe as a ‘newly ascendant model of ‘nature’, one swarming with organic operations unfolding at scales below everyday human perception, simultaneously independent of, entangled with, enabling of, and sometimes unwinding of human, animal, plant, and fungal biological identity and community.” This ecosystemic view of humans as entangled environments was metaphorically enshrined in the paper The Human Microbiome: Eliminating the Biomedical/Environmental Dichotomy in Microbial Ecology by microbiome research pioneers Ruth E. Ley, Rob Knight and Jeffrey I. Gordon, in which they write: “When a new human being emerges from its mother, a new island pops up in microbial space. Although a human lifespan is a blink in evolutionary time, the human island chain has existed for several million years, and our ancestors stretch back over the millennia in a continuous archipelago” (Ley et al., 2007, p. 3). Similarly, Scott Gilbert has written of what he calls a holobiont birth narrative, emphasizing the continuous communal and environmental embeddedness of individuals (Gilbert, 2014). Humans, from this perspective, cannot be understood as singular foregrounded entities standing against a backgrounded environment; they are themselves environments, embedded in and traversed by other environments larger and smaller.

This shift was, as Juengst and Huss (2009) describe, integral to the entire Human Microbiome Project (HMP), right from its inception. The researchers articulated a vision of the human genome as part of a human metagenome, which included the genomes of all the microbes associated with the body. The human body, it was argued, should be thought of as an ecosystem, and to be human was to be a superorganism consisting of multiple organisms that together produced a self. Bodies were environment for microbes, and microbes were environments for bodies. Thus, the thrust of the project was at once both methodological—using new technologies to study living things in new ways; and conceptual—re-organizing and re-describing the structure and function of the bodies in question.6

Despite the clarity of the HMP’s vision, defining and situating these multiple, entangled environments was a complicated affair right from the start. Early discussions around the project began with an informal brainstorming session in February 2006. Here, participants noted the many variables that would have to be taken into account in order to understand the microbiome: temporal, genetic, environmental, seasonal and individual factors. The question was also raised of what a normal or core microbiome might be, and if such a thing even existed. As Sangodeyi (2014, p. 264) discusses, the questions raised at these workshops were at once practical and philosophical: “What did a healthy body look like in microbial terms? Was there such a thing as a core microbiome? What was the difference between the microbiome in health and disease? These questions, central to the practicalities of research and study design, came down to a deceptively simple question that had deep cultural resonance: what did it mean to be normal? And what were the boundaries of health?”. Eventually, phase 1 of the project was structured according to distinct body sites with particularly rich and diverse microbial ecosystems: gut, skin, vagina, nose and mouth (The iHMP Research Network consortium, 2019). The groups working on the different sites each proceeded with different understandings of how to determine what a normal microbiome might be (Sangodeyi, 2014)—an indication of the complexity, variety and environmental embeddedness of the human microbiota.

2.2. A history of place neutrality

The tension between the inwards-oriented, programme metaphors of the Human Genome Project and the Human Microbiome Project’s reliance upon an ecological and environmental conception of human bodies also point to a deeper tension in the historical development of biomedicine. Environmental historian Christopher Sellers has argued that modern biomedicine derived a significant part of its conceptual rigor, analytical power and clinical efficiency by separating organism and environment (Sellers, 2018, p. 1). He terms this place neutrality, suggesting that from the late 19th century and onward into the 20th century, medicine and medical science increasingly aspired to “a medicine in which patients’ own places didn’t matter to what doctors thought or did” (Sellers, 2018, p. 1). Inspired by the increasing emphasis on the clinic and the hospital as the sites where medicine happened, was studied, and became conceptualised (Foucault, 1973), this new vision of medicine turned inwards. Disease became localised, and the interior landscapes of human bodies became the primary if not exclusive domain of the medical practitioner and the medical scientist (Jewson, 2009). Environment and body came to be conceptualised and studied at an increasing distance from one another.

This inwards move has to be understood in the context of medical theories and practices that it diverged from: it was quite distinct from mid-19th century and earlier medicine, which was built on a much more fluid ontology in which bodies and environments were in constant

---

5 Jann Sapp (2021) has recently written a biography of Joshua Lederberg, where he emphasizes Lederberg’s contributions to changing the narratives about microbes.

6 See Stengers (2020, p. 228) for an argument that metagenomics technology, born out of a need to accelerate reading of the human genome within the Human Genome Project, then became the “third-millennium microscope” for gazuing upon microscopic wilderness, bringing forth a “world overflowing from all sides the tranquil categories that ordered it intelligibly”.

---
exchange and bodies were far more porous and permeable. Neo-
Hippocratic atmospheric thinking, which dominated the 18th century and first half of the 19th century, emphasised environmental concepts as key ways to understand and intervene in disease. Even as anatomical knowledge was growing, and a more clinical pathology developing, medicine at that time still understood bodies through environmental ontologies (Nash, 2007) such as miasma—the theory that epidemic disease was caused by ‘bad air’ resulting from putrefaction. Airs, winds, weather, fluids and landscape topography were the keystones of this environmentally inclined medicine. By the mid-19th century, as medical statistics and the categorisation of pathologies were gaining increasing traction in medical thinking and practice, the lack of rigidity and causal explanatory power of earlier theories were increasingly visible, for example in understanding epidemic diseases such as cholera. Doctors began looking to more empirically focused theories of disease.

This new place neutral medicine was bolstered by the development and explanatory power of experimental physiology (Stahlschmidt, 2012). Pioneers such as Claude Bernard emphasised the body as having a self-regulating inner environment (Lanecker, 2017), and outer influences were increasingly seen as less relevant, pushed aside by the drive to understand the mechanisms of internal regulation. As experimental physiology began having effects on clinical practice and medical ontology, slowly at first and then much faster through successes such as germ theory, disease increasingly became a thing to be studied inside the body. Even as germ theory found the source of the disease in the environment, the clinician’s task began only once the patient was sick. The battle for health was fought by attempting to restore homeostatic balance within the patient (Sellers, 2018). Its explanatory power and its understanding of the interior terrain bolstered the success of this approach; a success that was achieved in part by the degree to which experimental, lab-based medical science managed to establish a space in which the mess of environmental conditions could be suspended. This suspension allowed the experimentalist to establish causal influences between organs, organ systems and disease. Medical science (and later biomedicine) thus had important origins in an epistemological push for control over, and separation of, environmental factors.

The environment outside the body was in this way rendered at a certain distance from interior life; body and environment were studied at a distance from one another. As Sellars argues, this was accompanied by the establishment of a number of more environmentally inclined medical sub-disciplines and specialties that studied relations between body and environment, but separated from the core medical faculties: tropical medicine, industrial health and public health. Sellers (p.1) writes: “The rise of place neutrality from the late nineteenth century onward, I suggest, had close and enabling historical ties to the near-simultaneous formation of place defined specialties—tropical medicine, bacteriological public health, and industrial medicine and hygiene.” This relieved other clinicians from having to consider environmental influences. Medical science as it developed in the 20th century was thus epistemologically and ontologically inclined towards place neutrality and transferability of knowledge across differing environments and different bodies. Medicine took place primarily within the body; as science, as clinical practice, and as a driving force in cultural articulations of health, illness and corporeal existence in general.

2.3. Microbiomes and the situated medical body

If the development of biomedicine in the late 19th and 20th centuries was marked by a remarkable shift in understandings of the inner workings of human bodies, the Human Microbiome Project marked both a practical and conceptual push towards shortening the distance between bodies and environments. Alongside this ontological impact of microbiome research, another major contribution has developed: as investigations into the human microbiome began in earnest, microbes were found to be involved in many of the major health issues facing post-industrial societies, such as metabolic, inflammatory, immune and systemic disorders (Lynch & Pedersen, 2016), as well as a range of mental disorders (Reider et al., 2017). These are all disease states sharply on the rise, as more and more countries experience major industrial advances and shifts towards urbanised living. The deep evolutionary microbial embeddedness and co-existence of humans with microbes has, it seems, been perturbed (Flandry et al., 2018).

Martin Blaser coined the expressions disappearing microbiota (Blaser & Falkow, 2009) and missing microbes (2014) to highlight the dangers of perturbation to this foundational co-existence. As the co-metabolism (Smith et al., 2013, p. 549) between host and microbiota is disrupted—for example, through widespread use of antibiotics and sanitisers, or through fibre-impoverished diets—the physiological integrity of the holobiont suffers. Indeed, Blaser (2014) argues that this loss of microbial (bio)diversity within and on our bodies is so pernicious that it surpasses in severity the dangers associated with the rise of antibiotic resistant pathogens such as Methicillin-resistant Staphylococcus aureus (MRSA) and Clostridium difficile.

Microbiome research, then, is in some sense a lightning rod within biomedicine and broader ideas about health vis-à-vis environmental thinking; it marks a deep concern with what geographer Jamie Lorimer has called a more probiotic understanding of the relationship between bodies and environment (Lorimer, 2020). While antibiotic attempts to manage life through control and separation had great impacts on public health and longevity during the 20th century, there is a now a growing sense that the unintended side effects on microbial ecologies are serious health disruptors. As Lorimer writes, “in recent decades, scientists and citizens have in many cases considered this antibiotic approach to be excessive; obsessions with purity, division, simplicity, and control lead to blowback and the emergence of new pathologies. Modern modes of managing life and the earth may be disturbing and intensifying natural processes, helping drive the planetary transition into the Anthropocene” (Lorimer, 2020, p. 3).

Thinking with microbiomes has also re-surfaced process approaches within philosophy of biology: questioning the adequacy to the present of metaphysical foundations of thought that have facilitated the categorical separation of organisms and environments. Under a process ontology, dialogical change is the foundation of all living processes, and stability becomes the phenomenon in need of explanation (Dupré, 2020). Organisms with their symbiotic microbiota—holobionts—are biological verbs, not nouns; products of lineage-forming entities collaborating in metabolism (Dupré & O’Malley, 2009). Boundaries and biological identities are formed and continuously re-formed in dynamic interactions. Here, the question of boundaries is rendered empirical: there are multiple ways of drawing boundaries between organism and environment, “reflecting real biologically salient aspects of the multiply interconnected systems that make up the living world.” (Dupré, 2012, p. 241).

In dialogue with a process ontology of life, anthropologists Niewöhner and Lock (2018) have proposed the notion of situated biologies. They

---

7 See Meloni (2019) for an account of the history of beliefs about plasticity within medicine, from ancient times to the postgenomic era.

8 See Chiu and Gilbert (2020) for an account of the constitutional role of fibre—as metabolised through microbiota—in the evolutionary history and physiological integrity of ruminant holobionts.

9 For a topical reflection on this, see Finlay et al’s (2021) analysis of how the Covid-19 pandemic might be influenced by microbiome factors as shaped by biosocial processes, and how COVID-19 disease and prevention measures may in turn affect the microbiome—with long-term biological and social outcomes.

10 The historical roots of process philosophy extend far back into antiquity, generally attributed to Heraclitus circa 500 BC, see Selby (2020).

11 For an early metabolic take on biological individuality, see Hans Jonas (1966), arguing that metabolism is not the boundary between outside and inside, but the very process that brings about that distinction.
point to the need to construe and document biologies as constituted in dialogue with place, objects, and through the materialization of ideas. Bodies as shaped through biomedical sanitation practices; bodies as shaped through cultural dining norms. And to include in our understanding of organismal biologies the impact of the very processes through which organisms (macro and microscopic) come to be known by humans—what Donna Haraway (1988) has called situated knowledge. Through interdisciplinary scholarly attention to microbiome research, boundaries of nature and culture blur; place and its practices become embedded in bodies that continuously individuate-in-relation.

This emphasis on the situatedness of knowledge is also finding echoes in recent calls to include more of the ‘wild’ into microbiome laboratory studies. To date, experiments with laboratory rodent microbiota have provided foundational knowledge about how hosts and microbiota interact under highly controlled laboratory conditions. However, these studies are built on the place neutral approach embedded deep in contemporary biomedicine. Summarised here by researchers calling for a re-wilding of laboratory studies: “The most convincing evidence for host-microbiome interactions has been gleaned through microbiome transplantation studies […] However, there is a trade-off: highly controlled experiments isolate mechanisms of interest, but they cannot simultaneously capture the full suite of ecological processes (drift, dispersal, competition etc.) that influence reciprocal host-microbiome interactions in nature” (Greyson-Gaito et al., 2020, p. 2). This points to the complex trade-off between experimentally verifiable microbiome knowledge gained through isolated laboratory conditions on the one hand, and the limitations on comparing and translating this knowledge into ‘the wild’ of human health.

Environmental complexity is thus a confounder, but also the stage on which the extraordinary variety of microbial-macrobiotic interactions evolve, acquire stability and de-stabilise. In a sense, microbiome research within biomedicine is struggling with questions of holism and embeddedness. Coming up against the limits of metrics of distinct parts and wholes; seeking ways to disentangle complex relational dynamics long enough to make distinct readings, even as the system continuously shifts. In interesting ways, this mirrors medical preoccupations before the advent of place neutral medicine: microbes as the new, empirically-grounded miasma.

3. Environmentality as a conceptual response

3.1. Introducing environmentality

In section 2, we situated microbiome research in a history of reaching for a more scientific medicine; a more controlled, precise and generalizable knowledge that would separate body from environment and locate it instead in the aperspectival ‘view from nowhere’ of the clinic. We argued that microbiome research challenges these core paradigms, rendering environmental factors more multiple and mutable than ever before. Attending to the microbiome makes foreground and background repeatedly switch place, and biological boundaries move. It blurs the biological boundaries between species and forces the environment (back) inside the clinic. We do not intend to play down the life-saving advances of clinical medicine, but rather to elucidate some of its current conceptual challenges (see section 4). As argued by Hannah Landecker (2019), categories such as inside/outside, organism/environment, are creaking under the weight of experimental data, bringing about a kind of ontological fracturing. It is not that categories dissolve, but that the data puts pressure on them; it becomes clear that, as thinking tools, they are not adequate to the multidimensional complexity of the living world.

In response to these conceptual challenges, we offer a concept that arises directly out of the ways that environment seems to shift around in microbiome research: environmentality as the state or quality of being a causal context for something else. This is a firmly perspective concept, to be used locally in relation to a particular case—a form of situated knowledge (Haraway, 1988). Aware of its own situatedness as well as the situated nature of its object of study. Cases can be diverse—e.g., a research paper, a clinical observation, or a scientific hypothesis. Within the case, environmentality invites us to start by foregrounding a particular entity, phenomenon or set of relations, and then to identify how surrounding entities or relations are acting as causal context for the foreground and vice versa, following lines of environmentality across time and space. What is backgrounded and what is foregrounded might shift as we follow a particular line of thinking, and new agents might be identified and brought into play. For example, in case study two, we begin by tracing the environmentality of the mother’s gut microbiome in relation to foetal development, and we end the analysis by foregrounding the role of fibre.

Environmentality addresses the proliferation problem, not by drawing tighter rings around usages of the term environment, but by side-stepping to see afresh what may already be there: the relational nature of the term environment itself, cutting across boundaries of time, space and scale. As Trevor Pearce (2010, p. 241) writes in his description of the term’s mid-19th century introduction by Herbert Spencer; “The word ‘environment’ seems to refer to a mishmash of unrelated entities: sunlight, soil, climate, air, organisms, and so on.” With environmentality, we don’t propose to give up on better understanding the ‘mishmash’, but to accept its originary looseness and underdetermination (Walsh, 2021) and then orient attention on a case-by-case basis to specific—and often surprising—realities within it. We have found value here in thinking alongside Niewöhner & Lock’s situated biologies (2018), which attend (anthropologically) to the particular ways in which place, practices and ideas become constitutive of biologies; the ways that environments become bodies across spatial and temporal dimensions—and, we add, across scales. We follow Niewöhner and Lock’s insistence that “what constitutes the ‘environment’ only becomes meaningfully defined in relation to a second entity to which that environment can be environment; or put in a different way—environment and environment always2 penetrate each other in several ways or co-construct each other” (2018, p. 691). See also Smith (2017) on this co-construction.

A related line of perspectival thinking is unfolding in the philosophy of biology around the question of what constitutes a biological individual. Suárez and Stencel (2020, p. 1310) have developed a part-dependent account of individuality whereby “holobionts are biological individuals from the perspective of the host, and ecological communities from the perspective of the microbes.” Dupré (2012) defends a promiscuous individualism, whereby boundary demarcation is decided in context depending on the biologically salient aspects of relevance to the current analysis. Lloyd and Wade (2019) have proposed the terms euholobiont and dembiont to demarcate differential adaptive consequences of the associations for hosts vs. for microbiota. We find kinship in the perspectival nature of these accounts, but work with a different focus. Rather than examining microbiota/organism relations in order to clarify what counts as an individual and from which perspective, we attend anew to the diversity and context-specificity of microorganisms/environment relations—and thus the kinds of things that can act as environment and for whom. That is to say, we are interested in encountering the relations that make an organism and an environment, rather than defining the entities between which those relations hold.

Environmentality is an epistemic or operational tool rather than an ontological one. It is a way of being attentive to causal factors and relations that may not obey categories such as inside/outside. Although kin in worldview to a process ontology (Dupré, 2020; Nicholson & Dupré, 2020)
3.2. Three case studies

Below we illustrate how environmentality has shaped our thinking in relation to three microbiome case studies, all based on biomedical research articles. The first exemplifies the ways in which foodstuffs travel into, become and exit bodies, acquiring environmentality in relation to the entities involved (Fernández et al., 2000). The second lays out how environmentality can help us construe microbe and human as co-metabolic partners within embryonic development in utero; a partnership negotiated through fibre (Kimura et al., 2020). And the third considers faecal microbiota transplants, in which a traditional waste product takes on environmentality for another, less ‘healthy’ environment (Wilson et al., 2019).

A paper by Fernández et al. 2020—A diet based on cured acorn-fed ham with oleic acid content promotes anti-inflammatory gut microbiota—provides an interesting case study for environmentality. This paper reports the results of a study designed to assess whether consumption of acorn-fed ham by laboratory rats may serve as a prevention strategy for development of ulcerative colitis. Specifically, whether a diet composed exclusively of acorn-fed ham (as opposed to standard feed) changes the susceptibility of laboratory rats to ulcerative colitis (UC) induced in the lab by the chemical dextran sodium sulfate.

The key entities in this study are acorn-fed ham and the inflammatory bowel disease ulcerative colitis. Acorn-fed or Iberian ham is produced from the muscle of free-range pigs who, in the months running up to slaughter, feed exclusively on acorns and grass in traditional agroforestry systems in southern Spain and Portugal. Acorns (the nuts of the oak tree), when metabolised by pigs, are considered to be of high nutritional value, as they contain high quantities of oleic acid, an anti-inflammatory fatty acid. Throughout months of feeding, the oleic acid content of the seeds becomes stored in the pig’s muscle tissue, creating a ham with a much darker colour, valued taste, and specific nutritional profile.

The interesting thing about this study for the purposes of our analysis is that the ‘environment’ travels through flesh across different scales, resulting in altered clinical outcomes. Agroforestry oaks produce acorns, which are eaten by the pig, whose muscle acquires an acorn-like quality, which is then consumed ad libitum for 7 days by rats (and their microbiota) in laboratory cages. The rats are then induced with ulcerative colitis for another 7 days and tested for disease index and gut microbiota composition—as compared to conspecifics fed on standard rat feed. With as many other clinical factors as possible controlled and standardised, disease activity indexes are traced back to the ‘acorn-like quality’ of the ham—its high oleic acid content. The acorn acquires environmentality in relation to the rat’s ulcerative colitis, as it is metabolised through the pig.

Here, what counts as environment—in clinically relevant ways—is amplified and simultaneously sharpened through an environmentality framework. Oak health; agroforestry systems; free-range pig production—as well as oak-fed ham and oleic acid and diet and gut microbiota—become environmental factors for inflammatory gut disease. Of course, many other entities have environmentality in relation to other entities in this study (e.g., the acorn/ham has environmentality in relation to the bacterial populations of the rat’s gut) but the foreground of our analysis rests on the acorn-pig-rat line.

The word environmentality is doing different work in the analysis from the work that the word environment—with its imbued imagery of immediate externality—can do. It would sound strange to argue that the acorn in the dehesa (the local agroforestry system) is an environment for the health of the laboratory rat. But the first has acquired environmentality (and explanatory value) in relation to the latter. It is this ability to hold and stretch thought across scales and temporalities, to follow circumscribed, case-specific, metabolic travelways that link environment-to-organism(s)-to disease (or health), that is of value. Thinking through environmentality facilitates a process of holding traditions of thought as foodstuffs move through (in this case) other foodstuffs to impact health outcomes. The analysis highlights that, for the purposes of health outcomes, ‘ham is not just ham’. That is to say, naming a foodstuff is not enough; its environmentality for health states will be dependent on provenance, on environmental and production factors. Switching the perspective, ham is also a different ham depending on circumstantial factors at the time of ingestion: e.g., gut microbiota ecology. As Lock (2017) argued, continual interactions of biological and social processes across time and space sediment into biologies that are local; they precipitate differently.

3.2.2. Not all mothers are equal in the metabolic afterlife of fibre

A paper by Kimura et al. (2020)—Maternal gut microbiota in pregnancy influences offspring metabolic phenotype in mice—provides another example through which to think alongside environmentality. The paper shows that, in a mouse model, short-chain fatty acids produced by the pregnant mother’s gut microbiota travel through the placenta to the foetus and influence development, making offspring less prone to metabolic disorders and obesity later in life. However, if the mother is fed a low-fibre diet during pregnancy, depriving the gut microbiota of fibre to metabolise and thus diminishing production of short-chain-fatty acids, mouse offspring are highly susceptible to obesity later in life.

The study indicates that the mother’s gut microbiota has environmentality in relation to the developing foetus, in mutual implication with the mother’s dietary intake. Put differently, the mother’s fibre intake acquires environmentality in relation to the foetus’ future susceptibility to obesity, but only in triangulation with the mother’s gut microbiota. In fact, the study shows that the protective effects of a maternal high fibre diet are cancelled when the mother is treated with antibiotics to eradicate gut microbiota. Similarly, supplementing germ-free or low fibre-fed females with short-chain-fatty acids during pregnancy resulted in adult offspring resistant to obesity. This indicates that it is the relational node between mother’s gut microbiota and mother’s fibre intake that acquires environmentality in relation to the offspring’s metabolic health.

The experimental layout was the following: pregnant mice were bred under control (SPF) and germ-free (GF) conditions, and pups were then raised by foster mothers to align post-natal growth environment. Upon weaning, the two groups were fed a high fat diet to induce obesity. The offspring of GM mothers were found to be highly susceptible to metabolic syndrome and developed an obese phenotype not seen in the control group. The authors postulated that short chain fatty acids (SCFAs) produced by the mother’s microbiota may have been travelling from mother to foetus via the placenta, influencing development of its metabolism.

13 We are not attempting to adjudicate on the clinical relevance of acorn-fed ham in relation to ulcerative colitis (e.g., it is interesting to note that SCF butyric acid levels usually associated with gut health were lower in the rats fed with Iberian ham treatment vs. standard feed, presumably due to lack of fibre in the diet). Rather, we are thinking environmentality through this study.
(this process would be impeded in a germ-free mother where there were no microbiota to produce SCFAs).

To further investigate the role of these SCFAs, a dietary intervention was performed. Non-germ-free mothers were fed low-fibre vs. high-fibre diet, and the susceptibility of offspring to metabolic syndrome was tested, as per the previous experiment. A low-fibre diet in the mother was found to render the offspring highly susceptible to metabolic syndrome, as had been the case with a germ-free reared mother. This indicates that microbial fermentation of the mother's dietary fibre is responsible for resistance to obesity in the offspring. To further investigate this, the authors conducted further studies supplementing low-fibre diet mothers and high-fibre diet, germ-free mothers with SCFA propionate during pregnancy. The resulting adult offspring were resistant to obesity as adults, indicating that the SCFAs were indeed responsible for influencing developmental pathway in the foetus in such a way as to render them metabolically healthy.

Where the first case study we reviewed indicated that not all ham is equal as an environmental factor in gut inflammatory disease, this study indicates that (otherwise identical) fibre is not equal as an environmental factor across different pregnant mothers—as its metabolism into SCFAs depends on the mother's gut microbiota ecology. It is the microbial fermentation, the relational node between mother's dietary intake and microbiota, that acquires environmentality in relation to obesity-resistance in the adult offspring. Fibre itself is only an environment in relation to the microbiota's metabolism; and vice-versa. We could say that the mother and her microbiota are held in reciprocal capture (Stengers, 2010), continuously re-actualised and re-negotiated through her dietary choices. And this relationship becomes part of the maternal metabolic communication with the foetus, influencing developmental pathways.

An environmentality line of thinking may help construe this. The 'external setting' association for the word environment makes it difficult to argue that a relational pathway is itself an environment. Thus, environmentality could help with relational interpretations of data, a need clearly arising within biological practice: e.g., see Human Microbiome Project phase 2's focus on interactivity factors between host and microbiota (The HMP Research Network Consortium, 2019). This need is also echoed within philosophy of science—for example, see Longino (2020) for a paper explicitly calling for interactivity as an ontologically distinct explanatory target in biology. And within interdisciplinary scholarship for example, Landecker and Kelty (2019) propose that we approach microbiome research from a metabolic interface angle: where the protagonists are not the humans nor the bacteria, but the metabolic products of their chemical relation, e.g., short-chain-fatty acids.

3.2.3. One stool does not fit all

Our final case study is a review paper by Wilson et al. (2019), which assesses the research on the phenomenon of super donors in faecal microbiota transplantation (FMT). FMT is the process of taking faeces from a healthy donor and transplanting either rectally or orally (in specialised capsules) to the colon of the patient. In a sense, attempting to restore a damaged environment by re-seeding it with a more healthy and hopefully beneficial microbial ecosystem (Young & Hayden, 2016). FMT has become widely utilised as a treatment for infection with antibiotic resistant Clostridium difficile, but there are also a growing number of studies examining its potential for treating other conditions associated with dysbiosis of the gut microbiota, such inflammatory bowel disease, irritable bowel syndrome, obesity, constipation, ulcerative colitis and also autism and other neurological disorders (Antonopoulos & Chng, 2016; Cryan et al., 2026; Sharon et al., 2019; Zhou et al., 2019). These

14 Stengers (2010, p.36) argues that “we can speak of reciprocal capture whenever a dual process of identity construction is produced: regardless of the manner, and usually in ways that are completely different, identities that coinvent one another each integrate a reference to the other (...).”

...
In the second case study (Kimura et al., 2020) we identified the relational pathway between the mother’s fibre intake and her gut microbiota to be an environment for the offspring’s metabolic health. Environmentality here helps us see that—just as not all ham is an equal ‘environmental’ factor for IBD (case 1) but is actually a process embedded in a production system—otherwise identical fibre is not equal in its environmentality to the metabolism of offspring of different mothers. Maternal fibre consumption acquires environmentality for the offspring’s future metabolic health in mutual implication with to the mother’s (localised, temporally dynamic) gut microbiota. Similarly, the mother’s microbiota acquires environmentality for the offspring only in triangulation with her fibre intake. In the final case (Wilson et al., 2019) environmentality helps us examine a currently unfolding clinical strategy—searching for super donors to provide stool for faecal microbiota transplants. Environmentality stretches the line between donor and recipient further back in time and across scales of microbial-human relations, helping to highlight the dependence of the transplant success on the specific interaction between donor and recipient microbiota; and revealing a possible clash of ethics between the super donor strategy and key insights of microbiome research.

In sum, environmentality helped us trace lines of relationality across scales, back in time, through flesh, and across organismic boundaries. In doing so, the ‘environmental factors’ at play became stranger and more embedded in matter, their effects dependent on the particular relations—alities at play. Ham is not just ham, fibre is not just fibre, a super stool is not super for everyone. This can potentially help us identify relevant configurations for deeper analysis, and to support the more relational, context-embodied thinking that both biology and medicine are reaching towards.

An environmentality analysis is a shift of perspective, a ‘making-strange’ that echoes the effect of microbiome research itself on our conceptions of organism, environment, health. It does not solve the challenge of proliferation, and in some senses could be said to recapitulate it, drawing still more entities and relations under the ‘environment’ umbrella. Our contention is that by doing so locally we can get a better picture of what counts; attending to the shape-shifting proliferation of reciprocal relations but with a constrained and case-specific focus. Environmentality does not define the specific kind of causality at stake in the relations it highlights, or place limits on the kinds of entities and relations that can enter into those relations. Causality here may be direct or indirect, and like environmentality itself, resides in a particular relation rather than being an essential, generalizable quality. Environmentality cannot deliver definitions of entities or relations that will apply across contexts and instances—it rather helps elucidate some of the reasons that definitions can be challenging in this field, and we hope can be a useful attentional tool, a sensibility whose strength lies partly in the efficacy (Stengers, 2008) of the word itself.

4. Discussion

In this concluding discussion, we revisit the landscape of microbiome research through the lens of environmentality. We return to the contrast between the genome and microbiome projects, and to the challenge of articulating relations between human and environment, showing how these disputed differences led us to environmentality. We bring to the foreground notions from Isabelle Stengers’ work that help us to articulate the concept and consider the kind of work it might do, and reflect on how environmentality has illuminated for us some of the conundrums facing biology and the health sciences. Finally, we argue that the distance between medicine and public health is shortened through microbiome research.

In section 2, we situated microbiome research and its proliferation of notions of environment in the context of an intellectual inheritance from the human genome project. We argued that the two projects—genome (HGP) and microbiome (HMP)—can be peers at through the metaphors they generated: informational in the first case, ecological in the second. One points to a human fully intelligible through its biology, a code to be deciphered; the other points to a human made strange through its biology, an environmentally porous new being that demands re-framing across disciplines. Stengers (2020, p. 228) has argued that the two projects actuate a contrast between the telescope and the microscope: the telescope allowing science to soar beyond earth-sensitive knowledge; the microscope opening up the realm of the small, a “world of teeming, swarming complicated activity” that overflows from all sides the tranquil categories that ordered it intelligibly.15

This contrast is of course a simplification. As Keller has argued (2020), the Human Genome Project (HGP) was most significant in its implications for our understanding of the relations between genes and genomes; and the rise of genomics has brought about a collapse in any framing of the genome as simply a collection of genes. Simultaneously, most (though not all) microbiome research within biology and biomedicine attempts to bring that “teeming, swarming, complicated”, earthly activity into cultivation in controlled laboratory conditions—re-taming into intelligibility those ‘escaped’ tranquil categories. Nevertheless, the transition into genomics and metagenomics marks a general transition in biology towards knowledge-in-interaction, Keller (2020) wrote that genomics research reveals, at every level, a biology which is itself constituted by interactions; and has proposed that genomes be construed as reactive systems (Keller, 2020)—an interesting interplay between circumstantial responsibility and constraint.

This metaphor of a reactive system points to a dynamic interplay between circumstantial responsibility and structural stability. The microbiome clearly has less structural stability than the genome—its composition varies widely within and across individuals and over time. Looked at in one way, it can be argued to be environment for the host—an environmental factor we have the power to intervene in (Knight, 2019). Looked at in another way, the microbiome is cast as part of the self. For example, Gilbert et al. (2012, p. 325) have argued that organisms “have never been individuals” by any criteria of individuality, whether anatomical, developmental, physiological, immunological, genetic or evolutionary. And Rees et al. (2018) have argued the microbiome is integral to all core categories traditionally used to define self—immune defence, higher functions of the brain, and genome.16 Thus the microbiome might be seen as a tentacular bridge, or rather millions of tentacular bridges, invisible to the naked eye, extending the human into environment and pulling the environment back into the body. In that understanding, our identity is now cast as woven in a mesh of reciprocal captures (Stengers, 2010) with microbes. A mesh that extends far back in evolutionary time but is also continuously re-actualised in our daily activities; our dietary choices; our chemical exposures; our intake of antibiotics and other drugs; our sanitation practices; our place dwellings; our social networks.

It is in the attempt to get a practical handle on the depth and complexity of these reciprocal captures, and their consequences for human health, that environmentality is useful for us. As we attempt to think through the particularities of cases where human healths and microbial lives entangle, the concept captures the contextual nature of environment without its gravitas towards the external and contiguous. It helps us to think processually across elements of a landscape (case study 1), across scales and generations (case study 2), and ecologies entangled through clinical practice (case study 3). For example, a line drawn across generations from a mouse mother’s fibre consumption to its offspring’s obesity travels across scales through the microbiota, as it acts metabolic processes and developmental cascades. Importantly for us, environmentality helps with the process of seeing and attending to relations and interactions across temporalities and scales, macro to micro. It acts as

15 A 2019 news feature in Nature (Watson, 2019) entitled The Trickster Microbes that are Shaking Up the Tree of Life is illustrated with a GIP that shows the Norse god Loki as ‘unruly microbes’, hacking at the base of the tree of life.

16 But see Parke et al., 2018 for a critical response.
an epistemological tool for thinking about particular situated cases where conceptions of environment are rendered strange through microbiome research.

Stengers (2020) introduces the notion of responsibility17 as a way of thinking about what is recognised as ‘real’ within biology, dictating what can be experimented upon and thus rendered intelligible. For instance, arguing that the microbes grown in Pasteur's laboratory were granted existing status, experimentally, because he was able to attribute to them responsibility for a broad range of other phenomena in the world: beer brewing, bread, epidemics. As microbiome research proliferates, so do such responsible entities. In the last decade, microbes have been attributed potential responsibility for an astonishing range of phenomena in human health, from ulcerative colitis to metabolic health, to evolution of the nervous system (Klimovich et al., 2018), and even to “control of brain development, function, and behavior by the microbiome” (Sampson & Mazmanian, 2015, p. 565). Yet it becomes increasingly clear that the living world does not fit neatly within our categories (of which microbes are one) and biology is, as Keller put it (2020), itself constituted of interactions. Furthermore, as we discovered in the case studies, the menu of responsible entities within microbiome research resisting full experimental intelligibility—a resistance reflected in translational challenges.

As microbes rise to visibility then, so do our structures of thought. It becomes clear, on the one hand, that the conceptual scaffolding we currently have for thinking the living world is not adequate to its complexity. The microbial world is, to borrow from Law (2016), baroque in sensibility—it overflows categories, changes and unfolds as we peer into its detail, and resists an overview. Incorporating its richness into our knowledge may require that we learn to think beyond categories—that we surround ourselves with tools and epistemologies for thinking beyond parts that add up to a neat whole (Latour & Weibel, 2020; Mol & Law, 2002). Process ontologies (e.g., Duprég & Nicholson, 2018) and metabolic thinking (Landecker, 2011; Landecker & Kelty, 2019) may come to our aid. As Latour and Weibel (2020, p.17) argue, “landing on Earth requires a different view of the material world than has been framed, delineated and entrenched since the modern period”. It is striking that this ‘different view’ is emerging as a perspectival one across many different disciplinary contexts. From the philosophical debate about biological individuals and holobionts (e.g., Duprég, 2012; Suárez & Stencel, 2020); to concepts such as situated knowledges (Haraway, 1998), the embedded body (Niewöhner, 2011) and situated biologies (Niewöhner & Lock, 2018); to proposals to overturn a “view from nowhere” imaginary of the planet (Arènes, 2018, p. 15); microbial metabolisms as material and metaphor in creative practices (e.g., Bencard et al., 2020); or calls for a more contextual public health (Cohn et al., 2013; Sariola & Gilbert, 2020).

It is clear that our concepts and structures of thought are shaken and stirred through the biological protagonism of the microbial. Furthermore, we see that concepts themselves have material consequences; that they are agents in the world. Landecker, thinking through the consequences of 20th and 21st century industrialisation of metabolism at a recent presentation, argues that our very concepts shape the biology we come to have: concepts sediment into bodies, into biologies and into societies. There is such a thing as the biology of history (Landecker, 2016)—antibiotic resistance is a case in point in the making. Tragically, so is the ongoing Covid-19 pandemic crisis. Microbes live and evolve in a world of human concepts—and alongside their histories, our own, and our healths.18 In a (bio)medical world, it becomes imperative that we attend to the medicine of history.

What, then, do we see when we look at contemporary medicine from the perspective of environmentality? Place neutral medicine derived much of its explanatory power from its ability to universalise and transfer knowledge and treatments across bodies. One patient's tuberculosis was functionally and categorically similar to another's. Everything was registered and diagnosed within the body. As the post-industrial health landscape shifts more and more towards disease states that are multifactorial and lifestyle embedded (obesity, allergies, autoimmune diseases, gut dysbiosis etc.), it is becoming increasingly vital to include environmental factors in understanding health and disease (Fuller, 2017). Indeed, the complex totality of the organism's environmentally enmeshed life is pushing its way forcibly into biomedical research. Microbiome research is one example, another is the emerging notion of the exposome (Wild, 2005), a term that refers to all the health-relevant exposures of an individual over their lifetime. Yet this fits somewhat uneasily with the thrust toward the development of therapeutic drugs to stave off and control the effects of these ‘lifestyle diseases’; and with the development of one-type-fits-most probiotics, prebiotics, and even psychobiotics.

Amidst incomplete knowledge, public health policy can play a role that clinical biomedicine, charged with offering individually-oriented therapies for identifiable conditions, cannot (at this moment) do. Whilst we still understand little of the complexities of causal pathways, we do know that the lives and healths of humans are profoundly implicated with the ecologies of their resident and neighbouring microbial communities. In public health, where the central unit is communities in situ, interventions can potentially be designed to nurture more probiotic environments (borrowing from Lorimer, 2020)—through policy, community engagement and cross-sector dialogue. As Greenhough and Lorimer have recently argued (personal communication, March 25, 2021), “microbiome research might call for a more provincial kind of understanding: How are healthy microbiomes configured through conjunctions of environmental conditions & cultural practices, carried out at particular places over generations?”.

In this paper, we have argued that microbiome research insists on the coconstitution of organism and environment: clinically relevant factors are obscured when an organism is extracted from environment or studied without reference to it. This is not a new insight—the problems of translation between laboratory animal studies and the real-world conditions they model, the difficulties of zoo breeding programs, and the intrinsinence of health inequities all speak to it. Yet the entanglements behind these difficulties are often treated as noise to be extracted, rather than as constitutive and a potential resource for understanding. This is often for good reason—to yield quantifiable forms of knowledge, or to deal with resource limitations or environmental degradation—but we argue that the time has come to foreground coconstitution and environmental embeddedness. The time is ripe for a more perspectival body: within biology, biomedicine and medicine.

A worm plucked from the soil and placed on the kitchen table cannot show us what it is and does; it is constituted via its ensainment with the soil microbiota, meteorological conditions, daily and seasonal cycles, but we do know that the lives and healths of humans are profoundly implicated with the ecologies of their resident and neighbouring microbial communities. In public health, where the central unit is communities in situ, interventions can potentially be designed to nurture more probiotic environments (borrowing from Lorimer, 2020)—through policy, community engagement and cross-sector dialogue. As Greenhough and Lorimer have recently argued (personal communication, March 25, 2021), “microbiome research might call for a more provincial kind of understanding: How are healthy microbiomes configured through conjunctions of environmental conditions & cultural practices, carried out at particular places over generations?”.

Financial support

This study was supported under a core group grant from the Velux Foundation, Denmark (00017008) to Louise Whiteley (PI) and Adam

---

17 Stengers (2020, p.229) makes clear that there are no moral connotations or accountability implied: it is “the act of identifying a responsible entity and assigning, imputing, attributing or refuting responsibility.”

18 See Sariola and Gilbert (2020) for an analysis of evolving microbial-human relations within a public health context.
Bencard (Co-PI), and a Novo Nordisk Foundation Mads Ølvisen Post-doctoral fellowship in Art and Natural Sciences to Adam Bencard (NNF17OC0024454). The work was also supported via internal funding from the Novo Nordisk Foundation Center for Basic Metabolic Research (CBMR), an independent research center at the University of Copenhagen partially funded by an unrestricted donation from the Novo Nordisk Foundation (NNF18OC0034900).

Declaration of competing interest

The authors declare no conflicts of interest.

Acknowledgements

We thank two anonymous reviewers for their detailed and generous feedback, which served to improve the manuscript and our articulation of the purposes of this article. Thanks also to Nikoline Nygaard for help with bibliography preparation, and to the Microbes on the Mind research group at Medical Museion for discussions that contributed to the development of this paper.

References
