FEMS Microbiology Reviews, 2024, **48**, fuae008
DOI: 10.1093/femsre/fuae008
Advance access publication date: 29 February 2024
Review Article

Life at the borderlands: microbiomes of interfaces critical to One Health

Simon R. Law[1,2,‡], Falko Mathes[1,3,‡], Amy M. Paten[1,4,‡], Pamela A. Alexandre[1,5], Roshan Regmi[1,6], Cameron Reid[1,7], Azadeh Safarchi[1,8], Shaktivesh Shaktivesh[1,9], Yanan Wang[1,10], Annaleise Wilson[1,11], Scott A. Rice[1,12], Vadakattu V.S.R. Gupta[1,6,*]

[1]CSIRO MOSH-Future Science Platform,Australia
[2]CSIRO Agriculture and Food, Canberra, ACT 2601, Australia
[3]CSIRO Environment, Floreat, WA 6014, Australia
[4]CSIRO Environment, Canberra, ACT 2601, Australia
[5]CSIRO Agriculture and Food, St Lucia, Qld 4072, Australia
[6]CSIRO Agriculture and Food, Urrbrae, SA 5064, Australia
[7]CSIRO Environment, Urrbrae, SA 5064, Australia
[8]CSIRO Health and Biosecurity, Westmead, NSW 2145, Australia
[9]CSIRO Data 61, Clayton, Vic 3168, Australia
[10]CSIRO Health and Biosecurity, Adelaide SA 5000, Australia
[11]CSIRO Health and Biosecurity, Geelong, Vic 3220, Australia
[12]CSIRO Agriculture and Food, Westmead, NSW 2145, Australia
*Corresponding author. CSIRO Agriculture and Food, Locked Bag 2, Glen Osmond, SA 5064, Australia. E-mail: Gupta.Vadakattu@csiro.au
‡Joint first author
Editor: [Andrew McBain]

Abstract

Microbiomes are foundational components of the environment that provide essential services relating to food security, carbon sequestration, human health, and the overall well-being of ecosystems. Microbiota exert their effects primarily through complex interactions at interfaces with their plant, animal, and human hosts, as well as within the soil environment. This review aims to explore the ecological, evolutionary, and molecular processes governing the establishment and function of microbiome–host relationships, specifically at interfaces critical to One Health—a transdisciplinary framework that recognizes that the health outcomes of people, animals, plants, and the environment are tightly interconnected. Within the context of One Health, the core principles underpinning microbiome assembly will be discussed in detail, including biofilm formation, microbial recruitment strategies, mechanisms of microbial attachment, community succession, and the effect these processes have on host function and health. Finally, this review will catalogue recent advances in microbiology and microbial ecology methods that can be used to profile microbial interfaces, with particular attention to multi-omic, advanced imaging, and modelling approaches. These technologies are essential for delineating the general and specific principles governing microbiome assembly and functions, mapping microbial interconnectivity across varying spatial and temporal scales, and for the establishment of predictive frameworks that will guide the development of targeted microbiome-interventions to deliver One Health outcomes.

Keywords: biomes; biofilms; omics; multi-omics; host; environment

Introduction

The interface between neighbouring ecosystems represent a confluence of unique habitat characteristics including nutritional resources, physiochemical processes, and environmental properties (Naiman and Décamps 1997). These liminal spaces, the borders of which shift over broad spatial and temporal scales, are often referred to as *ecotones*, a term used to describe the tension existing between adjacent ecological systems and host environments. Frequently, these interfaces will support greater rates of speciation and more diverse biological communities with complex interactions than the sum of the two neighbouring ecosystems would predict (Kark and Van Rensburg 2006). Additionally, these boundary regions act as portals for the movement of organisms between discrete ecological compartments (Álvarez-Garrido et al. 2019), a feature that is especially true for microorganisms, whose metabolic versatility and resilience enable many to thrive across a diversity of hosts and environments (Meyer-Dombard et al. 2011, Raymond and Alsop 2015). At the microscopic scale, microbial interfaces may be physical (e.g. the root–soil interface of the rhizosphere or the respiratory tissue–air boundary) or functional (e.g. bidirectional relationships of the gut–brain axis or root–phyllosphere). These interfaces can connect disparate microbial and microfaunal communities, and facilitate the exchange of nutrients, energy, and genetic material; while serving as a cauldron of selective pressures that block the migration of specific microbes (e.g. human skin, with its acid mantle, immune cells, and antimicrobial peptides shield the body from pathogens).

Over the past two decades, the field of microbial ecology has grown considerably, in part driven by advances in nucleic acid sequencing approaches that have enabled culture-independent and community-level interrogation of microbial taxonomy, function, and host interactions. This new paradigm has repositioned microbes as foundational organisms within global ecol-

Received 26 July 2023; **revised** 12 February 2024; **accepted** 27 February 2024

ogy: from the provision of essential ecosystem services linked to nutrient cycling, food production, carbon sequestration, greenhouse gas emissions, and ecosystem health; to their intimate relationship with plant, animal, and human health. Further, microbes functioning at submicrometre levels can have significant consequences at global scales through the production and consumption of greenhouse gases (Tiedje et al. 2022). The growing recognition that human health is intrinsically tied to the health of the environments we inhabit and the organisms we share them with has given rise to the concept of *One Health*, defined by the World Health Organization as "an integrated, unifying approach to balance and optimize the health of people, animals and ecosystems" (www.who.int). The emergent complexity of this dynamic and interconnected system–populated with organisms from every branch of the tree of life, exercising every possible trophic strategy–challenges modelling efforts aimed at predicting the impact of global, regional, or microscopic perturbation on vital ecosystem services and human health.

Bacteria inhabit and thrive in almost every habitat on the planet, from the deepest ocean sediments to the highest mountains and are even present in upper reaches of the atmosphere. These organisms are not only ubiquitous but are extremely versatile in their ability to generate energy for cellular processes as well as capturing nutrients needed for persistence and reproduction. As such, bacterial metabolism is responsible for all of the major biogeochemical cycles on the planet. Indeed, without their function, life on Earth would cease. Not surprisingly, this metabolic versatility has enabled bacteria to evolve intimate relationships with other organisms, where they are associated with enhanced function of that system. For example, microbial activities at the root–soil interface (rhizoplane) are well-known for their role in enhanced plant nutrition and health and overall production (Gupta and Sharma 2021). Given their intimate relationships with most habitats and hosts on the planet, it is not surprising that there is considerable interest in studying how microbes mediate these effects both in terms of their physical interaction and functional connectivity. This is challenging due to the diversity and complexity of these microbiomes and hence, many studies have focused on individual organisms in the context of their specific biomes. Despite being keystone components of this complex system, microbial ecotones remain understudied, likely due to difficulties in obtaining representative samples from systems with dynamic spatial and temporal boundaries, and technological limitations associated with capturing the multiplex interactions and processes that occur within them. However, it is clear that functional microbiomes are the sums of the many species (even phylogenetically diverse groups), that not only interact with their theatre of activity, but also interact with other species. Thus, it is essential to consider the microbiome *in toto* rather than specific individuals in isolation. Further, the species in these microbiomes may be distantly related, but nonetheless provide similar ecosystem services, known as functional redundancy. In this way, it is also clear there is a need to study such communities with an understanding of the essential function of the community in relation to the biomes to better understand the drivers of ecosystem health and function.

This review will first address microbial interfaces through a lens of One Health: first defining the distinct microsites of microbiome and host or environment interactions or "theatres of activity" critical to One Health: soils, the root, the ruminant, and human gut and subsequently will discuss how colonization of those sites, biofilm formation, occurs. Next, we will address the different components of host–microbe interactions at these interfaces in terms of generalizable principles, such as factors that drive microbial community assembly, mechanisms of microbial attachment, growth and succession, and the effect these processes have on host function and health (Fig. 1). The review will then evaluate current and emerging technologies and modelling approaches that will facilitate a greater understanding of microbiomes in– and across–specific niches and how they interact with their host as well as predict functional outcomes. The review will conclude with current state of the art as well as new and emerging approaches to modification of the microbiome for improved and strategic outcomes.

Microbial interfaces critical to One Health

Soil surfaces

Soils serve as global and dynamic reservoirs of microbial diversity, making them both providers of essential ecosystem services that can strengthen global food security and mitigate anthropogenic impacts (climate change and soil pollution), as well as sources of devastating pathogens and antibiotic resistance genes (Zhu et al. 2019). As such, there is increasing pressure to more firmly entrench soil health into the broader One Systems Health approach (Banerjee and van der Heijden 2023, Singh et al. 2023). This represents an enormous challenge, as a single handful of healthy soil contains more microorganisms than all the human beings that have ever lived (~117 billion) and yet, due to its enormous surface area, far less than 1% of soil surfaces are actively colonized by microbes (Young and Crawford 2004). These communities are not evenly distributed, but instead form transient biofilms in soil pores and aggregates that wax and wane spatially in response to a variety of factors. Complicating matters further, only a small fraction of this microbial diaspora is metabolically active and contributes to physiochemical processes at a given point in time, as microbial dormancy facilitates the persistence of community members over extended periods of unfavourable conditions (Lennon and Jones 2011).

The root surface

Roots are the plant's primary site of nutrient and water acquisition, and its exposure to microbial life; necessitating the plant to carefully navigate an assortment of immunological, nutritional, and symbiotic signals to optimize its own growth, health, and development. Several studies have estimated the total surface area of root systems in a variety of species and environments to far exceed aboveground plant surface area (Jackson et al. 1997, Butler et al. 2013, Urban et al. 2015). Thus, the intersection between plant roots and the surrounding soil (known as the *rhizosphere*) represents a truly enormous theatre of activity for soil microbes, and can be viewed as a semicontinuous ecotone between the interior of the root (the *endosphere*; including cortical and endodermal cells), the root surface (the *rhizoplane*; including root epidermal cells and secreted mucilage), and the thin layer of soil surrounding the root (the *ectorhizosphere*). Microbial diversity has been shown to decrease dramatically between the ectorhizosphere and the interior of the root (Trivedi et al. 2020), highlighting the critical gating role played by the rhizoplane in regulating microbial entry into the root. Additionally, microbial community composition has been shown to differ significantly between the roots of different plant species (Chaluvadi and Bennetzen 2018), different root types within the same plant species [e.g. seminal or nodal roots; (Kawasaki et al. 2016), and even along the axes of a single root (Kawasaki et al. 2021)].

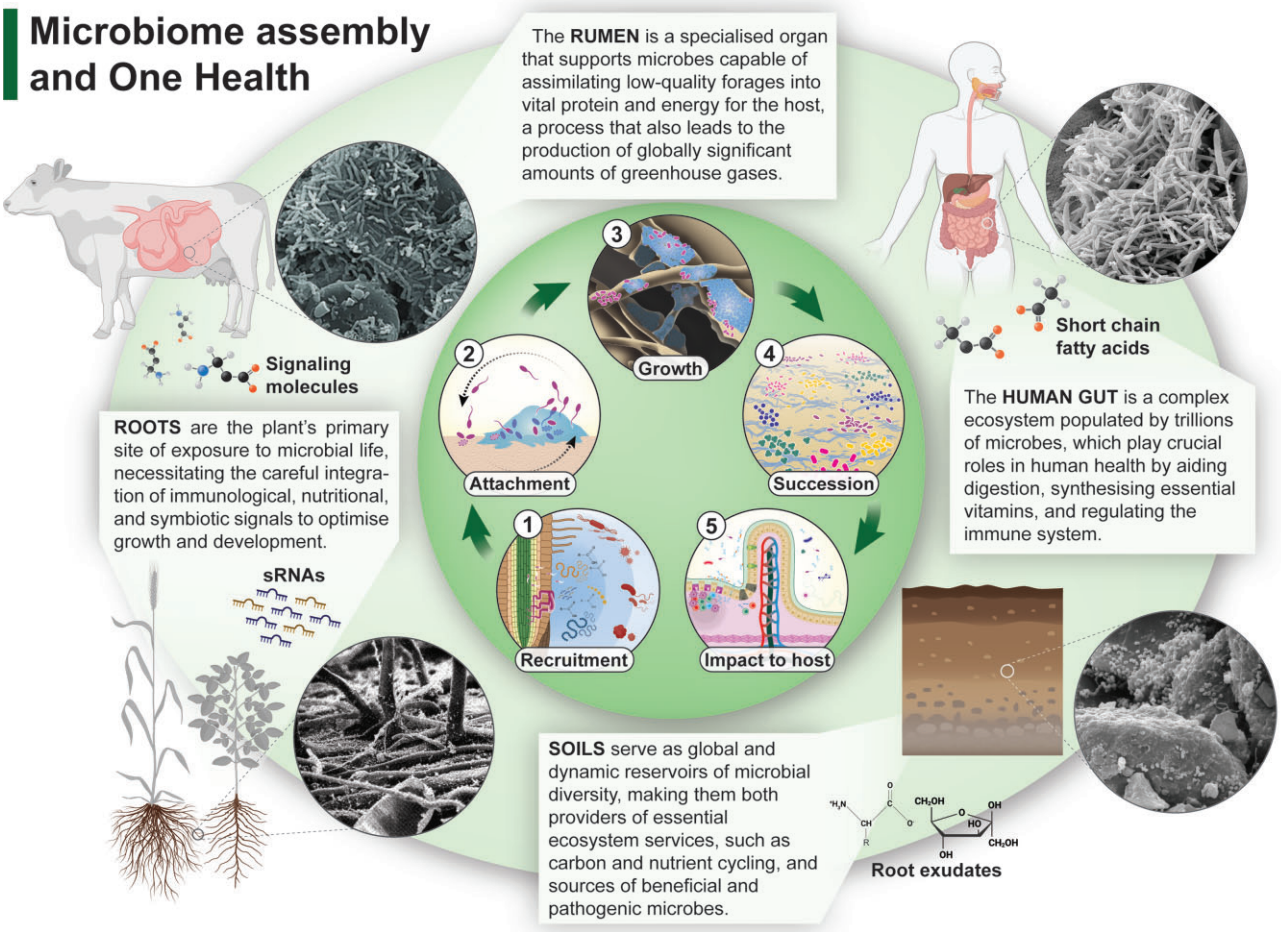

Figure 1. Core principles of microbiome assembly and function across host and environmental interfaces that are critical to One Health. The outer circle represents the hosts and environmental interfaces that are critical to One Health, including soils, the plant root, the rumen, and the human gut. A representative electron micrograph displaying microbial community colonization at each interface has been provided. The inner circle represents the conserved sequence of events that enable the formation of microbial communities on host or environmental interfaces. *Recruitment* can be via vertical or horizontal transmission and relates to the behavioural and physiological strategies employed by the host to gain access to, selectively attract, and incentivize the beneficial microbes. *Attachment* to host and environmental interfaces is governed by fundamental physical, chemical, and biological processes that enhance the survival and colonization of microbes. *Growth and Succession* encompass a multitude of complex microbe–microbe and microbe–host/environment interactions in the developing communities, resulting in beneficial or detrimental outcomes. *Impact on Host (Host response)* reflects the influence the microbiome has on shaping aspects of the host phenotype, nutrition, and health, such as developmental trajectories, immunity, longevity, and behaviour.

The ruminant gut

The almost 4 billion domestic ruminants (O'Hara et al. 2020) in the world synthesize energy from low-quality forages via microbial fermentation in a specialized foregut chamber, the rumen. There, carbohydrates and nitrogen-containing compounds are either assimilated into microbial biomass or fermented into volatile fatty acids (VFA) that are absorbed into the bloodstream. The microbial proteins are vital for the host muscle and milk synthesis (Bach et al. 2005), while VFAs can supply up to 70% of the host's energy requirements (Bergman 1990). Microbial composition in the rumen varies with diet, age group, breed, and geographical location (Henderson et al. 2015, Dixit et al. 2022). It is a functionally redundant community of bacteria, fungi, methanogenic archaea, ciliate protozoa, and viruses with cellulolytic, hemicellulolytic, amylolytic, proteolytic, and lipolytic activity (Morais and Mizrahi 2019). Differences in rumen microbiome profiles have been associated with economically and environmentally important traits such as feed efficiency (Xue et al. 2022, Zhao et al. 2022b), methane emission (Ramayo-Caldas et al. 2020, Cardinale and Kadarmideen 2022), and milk composition (Stergiadis et al. 2021). In contrast, the role of the lower-gut microbiota in ruminants' health and production has not been extensively studied. However, it was shown to influence traits such as feed efficiency (Welch et al. 2020), milk production (Monteiro et al. 2022), and immune response (Malmuthuge et al. 2013). This is partially because the large intestine is a site for microbial fermentation of the remaining fibre and other complex polysaccharides, but importantly, it is also a highly active region in terms of immune function and has a crucial role in the production and metabolism of hormones, neurotransmitters, and other bioactive compounds that can influence host health including physiology, behaviour, and stress response (Freestone and Lyte 2010, Du et al. 2023).

The human gut

In humans, the gastrointestinal (GI) tract is one of the largest interfaces (250–400 m^2) between host and microbes, which harbours

about 100 trillion microorganisms (Thursby and Juge 2017). This complex and dynamic population of gut microbiota plays a critical role in human health (Ursell et al. 2012). Bacterial colonization is vital for maintaining the structure and function of the human GI tract, development of the mucosal immune system, and breakdown of nondigestible nutrients (Jandhyala et al. 2015). The established bacteria interact with other microbes to form the gut ecosystem, which forms a symbiotic relationship with the host under normal circumstances (Jansma and El Aidy 2021). However, many factors can challenge the homeostasis and lead to imbalanced gut microbiota, such as infection with pathogens, antibiotic use, unhealthy diet and lifestyle, and other environmental factors.

Examples of other interfaces that provide suitable habitats for microbiome–host or microbiome–environment interactions include the skin–environment (air, soil, and water), water–sediment, phyllosphere–environment, mucosa–environment and so on, but are not the focus of this review.

Biofilm formation

The process of biofilm formation and its consequences have been well-reviewed over the past few years; thus, this section will present some of the salient features of biofilms relevant to microbiomes and their role in One Systems Health. Specific mechanisms and consequences of biofilms in relation to the ecotones they inhabit will be discussed separately, below. Biofilms are ubiquitous across Earth's biomes with relevance for human, animal and plant health, terrestrial and aquatic ecosystems, as well as natural and human-made surfaces (Flemming et al. 2016, Sentenac et al. 2022). They can be found at the interfaces between plant roots and soil, lumen and gut wall (in both, rumen and human), food particle and lumen, oral biotic/abiotic surface, as well as those that are immersed at solid–liquid interfaces such as rocks, sand grains, decaying wood, and so on. (Flemming and Wuertz 2019, Sentenac et al. 2022). Thus, the formation of a biofilm may be one such universal trait associated with microbiome members. Biofilms are generally described as the sum of the microbial species present as well as the three-dimensional extracellular matrix (e.g. polysaccharides, proteins, lipids, and extracellular DNA) that holds them together and enables the establishment of many of the emergent properties of biofilms. A constant and dynamic dialogue between the biological and physical forces modulated by microbiome members and host/environment have been suggested to shape and maintain microbial biofilms (Wong et al. 2023).

While biofilms are predominantly studied in the laboratory as mono-species systems, in natural and engineered habitats, they almost always are comprised of multiple species and these biofilms may be attached to a substratum, such as soil particles, the root surface or intestinal wall, or may be aggregates that are bound together but floating in an aqueous environment, such as biosolids in wastewater treatment plants or marine snow, and the lumen of the human gut. The presence of multiple species in a biofilm community also means that the number of functional genes present in the community scales with the number of different species present and gives the community an expanded metabolic and phenotypic potential. For example, analyses of the diversity of 1073 *Pseudomonas* genomes found 200 839 protein-coding gene families encoded in the pangenome (Jun et al. 2016), while a *Bacillus* pangenome size of 155 747 genes was reported from only 20 genomes (Alcaraz et al. 2010). Given this expanded "community genome" it is also recognized that biofilm formation has several beneficial consequences for the associated bacteria, such as increased stress tolerance (e.g. predation; Queck et al. 2006) and antibiotic resistance (Yan and Bassler 2019), enhanced nutrient acquisition, as well as habitat modification and facilitating species interactions. For example, *Pseudomonas aeruginosa* was demonstrated to confer surfactant tolerance to two co-occurring species that were individually sensitive to the surfactant (Lee et al. 2014). Similarly, mixed species communities have enhanced metabolic potential, which can be harnessed for the remediation of contaminated soils (Li et al. 2020). The process of biofilm formation has also been well studied and represents a life cycle, where bacteria colonize a surface, develop into a mature structure and then disperse to colonize new sites. Further, biofilm formation facilitates interaction and enables niche habitat modification (e.g. reduced O_2 tension through respiration to enable anaerobes to grow in an otherwise aerobic habitat).

In the One Health context, biofilms may facilitate the transfer of bacteria between systems or biomes. For example, bacterial biofilms on the surface of fresh fruits and vegetables can be transmitted to the gut of humans and animals. These newly introduced communities have the potential to then disturb the existing microbiome through invasion or displacement of the existing "healthy" community. This disturbance may lead to a new stable state for the gut community, which may have healthy or disease-promoting impacts. Additionally, these ecotone-associated communities may also transfer both beneficial and deleterious functional genes from one habitat to another e.g. antibiotic resistance genes transferred from one habitat to another potentially contributing to the spread of resistance, or enhanced competence of specific members of the oral microbiome when the biofilm undergoes stress. While the process of biofilm formation may be fairly generalizable, the specific factors that facilitate microbes to coalesce as a community around a host or specific habitat are often quite specialized. Below, we will explore the primary processes that drive microbiome establishment around their host, i.e. recruitment, attachment, growth, succession, and impacts to the host.

Microbial recruitment at the interfaces

The prevailing attitude that microbial symbiosis is an elementary principle of all organisms is being increasingly challenged by growing reports of organisms with transient or completely absent microbiomes (see Moran et al. 2019 for an excellent review). However, in the case of most organisms, whose healthand development rely on the vital contributions of a resident microbiome, it becomes crucial to employ various behavioural and physiological strategies aimed at (i) gaining access to beneficial microbes, for example, via seed, vaginal delivery, and breastfeeding, (ii) selectively attracting advantageous microorganisms, such as through the secretion of plant flavonoids to entice nitrogen-fixing rhizobia, and (iii) incentivizing the growth of beneficial microbes, for example, by providing them with essential nutrients like photosynthates in the case of root-associated symbionts. These strategies, collectively known as microbial recruitment, can be vertical in nature (e.g. the transmission of microbes from parent to offspring) or horizontal (e.g. the transmission of microbes from environmental sources) and serve to increase the likelihood that only those with desirable traits (e.g. an enzymatic repertoire that can extend the host's metabolism or pathogen-suppressing activities) are selected from the highly diverse pool of microbes present in the environment. The term "recruitment" in the human and animal gut environments generally denotes to "seeding or colonization" as the gut is not an open system and the recruitment process

in the gut is more passive rather than active. It is also important to note that ongoing microbial recruitment is impacted by the host's extant microbiome, as newly recruited microbes may benefit from the habitat-facilitating activities of early colonizers or be competitively excluded by microbes with similar ecological requirements (Darcy et al. 2020).

Sources and mechanisms for microbial recruitment

Several recent studies have shown that a sizeable proportion of the microbes that inhabit plant roots, especially in seedlings during early colonization, are inherited in the form of seed-borne endophytes, particularly bacteria of the genera *Bacillus* and *Pseudomonas* (Truyens et al. 2015, Abdelfattah et al. 2021, Moroenyane et al. 2021). This vertical transmission occurs via vascular connections with the maternal plant or harboured within the male gametes (pollen; Frank et al. 2017) and provides beneficial microbes with priority effects that enable the establishment of founder populations, with profound implications for downstream microbiome assembly and niche partitioning in the adult plant (Toju et al. 2018). Despite this, plants also have an impressive capacity to modify their environment to cultivate beneficial microbes or hinder disease-causing pathogens, through a process known as rhizodeposition (Carrión et al. 2019, Kawasaki et al. 2021). The best described example of this is root exudation, which involves the delivery of up to 30%–40% of a plant's photosynthetically fixed carbon into the soil (Whipps 1990), predominantly in the form of primary metabolites (e.g. sugars, amino acids, and organic acids) and bioactive secondary metabolites (e.g. flavonols, glucosinolates, and indole compounds). Primary metabolites represent a valuable source of energy and nutrients for soil microbes and promote the selective proliferation, and thus recruitment, of a subset of the bulk soil community into the rhizosphere. In contrast, specialized secondary metabolites, amongst many other roles, mediate the molecular dialogue between the root and symbiotic microbes. For example, root-secreted flavones attract nitrogen-fixing rhizobial species and can initiate their presymbiotic programming (Compton and Scharf 2021), while strigolactone-rich exudates promote symbioses with arbuscular mycorrhizal fungi (Banasiak et al. 2020). In addition to soluble secondary metabolites, recent interest has turned to root-emitted volatile organic compounds (VOCs), which serve as potent chemoattractants of beneficial bacteria and, due to their unique physiochemical properties, can readily diffuse across gas- and water-filled pores and greatly increase the effective range of root microbial recruitment (Schulz-Bohm et al. 2018). Plant-secreted VOCs have also been demonstrated to signal neighbouring plants to alter their root exudate composition to effectively synchronize root microbiomes across neighbours (Xiao et al. 2021). In response to these chemical signals, soil microbes employ a variety of chemotactic strategies to migrate to the root. For example, while sessile bacteria (e.g. the spores of *Streptomyces* spp.) may stochastically translocate via the passive flow of water through the soil pore matrix, they may also tether themselves to motile bacteria or fungal hyphae, affecting a form of microbial hitchhiking (Muok et al. 2021). Bacterial appendages, such as flagella, enable motile microbes (e.g. *Bacillus subtilis*, *Rhizobium leguminosarum*, and *Azospirillum brasilense*) to swim through water-filled pores and liquid films, or swarm across solid surfaces towards the origin of the chemoattractant (Jarrell and McBride 2008). Microbes employing filamentous growth forms (primarily fungi but also some Actinobacteria) have a distinct advantage over motile bacteria, as their mycelia can span air-filled spaces, a feature that is especially useful under unsaturated (low connectivity) soil conditions (Wolf et al. 2013).

Despite physiological and morphological differences between humans and ruminants, the maternal microbiota reservoir is the primary source for the initial microbial recruitment for both organisms (Wang et al. 2020, Liu et al. 2023). However, the timing of microbial recruitment, whether it begins in prenatal intrauterine locations or during and after delivery is debatable in both humans (Kennedy et al. 2023, Xiao and Zhao 2023) and ruminants (Hummel et al. 2022). Low biomass and low diversity of microbes and microbial signals have been reported in human and ruminant foetus (Stinson et al. 2019, Guzman et al. 2020, Amat et al. 2022), but currently, there is no evidence supporting the presence of stable and abundant colonizers in a healthy foetus under normal circumstances (Kennedy et al. 2023). A few studies suggest that the maternal gut, vagina, and oral cavity could potentially serve as sources for seeding the foetal microbiome via the placenta during pregnancy (Aagaard et al. 2014, Gomez-Arango et al. 2017, Wang et al. 2021a, Hummel et al. 2022, Xiao and Zhao 2023). A study in sheep, investigating the routes through which nonpathogenic bacteria can enter the foetus, was unable to recover live bacteria from foetal tissue (Yu et al. 2021). However, the same study showed that DNA and proteins derived from bacteria introduced into the maternal mouth could be detected in the foetal brain and trigger alterations in foetal gene expression, representing an intriguing avenue of communication between the foetus and its mother's environment, and a potential mechanism to ready the foetus for ex-utero life. So far, the exact mechanisms and routes of microbial migration from the mother's body parts to the womb remain unclear.

Regardless of the uncertainty of intrauterine microbial recruitment, the main recruitment of early life microbes occurs during birth when the baby passes through the birth canal and encounters maternal vaginal and colonic microbiota (Walker 2017). After birth, neonates continue to recruit microbes via breast milk and skin-to-skin contact with the mother (Pannaraj et al. 2017). This vertical transmission is essential for the development of a healthy intestinal tract both for humans and ruminants (Zhang et al. 2021a). In fact, during the first few weeks after birth, infants and calves are the most similar in terms of digestion, as liquid feed ingested by preweaned ruminants bypasses the rumen through the oesophageal groove and is digested and absorbed in the small intestine. Under optimal colonizing conditions, early acquired human microbes include *Bacteroides*, *Bifidobacteria*, and *Lactobacillus* (Walker 2017, Kim and Yi 2020), which play important roles in the development of protective immunologic functions (Walker 2017). Similarly, in milk-feeding calves, *Bacteroides*, *Lactobacillus*, and in particular *Bifidobacteria* were shown to quickly become the dominant bacterial groups after birth, replacing initial aerobic and facultative anaerobic bacteria (Rada et al. 2006, Vlková et al. 2006, Zhang et al. 2021a). Horizontal transmission also occurs in the initial stage of life through the surrounding environment, nonbreastfed feeding practices, and interactions with nonmother individuals.

Challenges to microbial recruitment

Recruitment is the first step of microbiome assembly across a variety of microsites, therefore, even minor disturbances to this process can impact the structure and function of the resulting microbial community, with significant consequences for the host's health and development. For instance, factors challenging a healthy maternal microbial community (e.g. overall health, im-

mune status, stress levels, nutrition, and exposure to antimicrobial compounds) or limiting the exposure of neonates to this vertical mode of transmission (e.g. caesarean section, alternatives to breastfeeding) are likely to impact early-life microbial establishment. In addition, challenges related to environmental disturbances (such as invasive agricultural practices and climate change), microbial competition for resources and niches, and disruptions due to the use of antimicrobials and other chemicals, can impact horizontal transmission. On the other hand, recruitment also presents a valuable opportunity for early targeted interventions to improve health and productivity, for instance using probiotics. However, evidence of long-lasting effects of these interventions are still scarce, suggesting that probiotic strains are rarely effectively recruited or retained when introduced into the gut.

The widespread use, and occasional misuse, of antimicrobial products across broadacre agriculture (e.g. seed dressing with fungicides; Zaller et al. 2016), livestock husbandry (e.g. prophylactic use of antibiotics; Low et al. 2021), and clinical settings (e.g. indiscriminate antibiotic use; Antunes et al. 2011), can have profoundly negative consequences on the vertical and horizontal transmission of microbes. First and foremost, antimicrobials can greatly decrease the abundance and diversity of microbes available for horizontal recruitment (Karlsson et al. 2014), as their modes-of-action invariably have nontarget effects that fail to discriminate between beneficial microbes and target pathogens. The consequence of this is particularly apparent in agricultural soils, where the frequent use of fungicides and herbicides can lead to the accumulation and persistence of active residues that are toxic to plant mutualists, such as mycorrhizal fungi and nitrogen-fixing rhizobia (Hemida Abd-Alla et al. 2000, Khan et al. 2020). Antimicrobials can also impact the vertical transmission of microbes. For example, in perennial ryegrass, foliar applications of fungicide were shown to reduce the vertical transmission of *Epichloë festucae*, an agriculturally significant fungal endophyte that can protect plant hosts from insect herbivory (Chynoweth et al. 2012, Ruppert et al. 2017). In humans, antimicrobials are widely used before and after birth, with up to 30% of mothers in developed nations receiving intrapartum antibiotic prophylaxis to prevent early-onset group B streptococcal infection in newborns during vaginal delivery (Moore et al. 2003, Cox and Blaser 2014). Using metagenomic approaches, Li et al. (2021) showed that perinatal antibiotic use resulted in an almost 50% reduction in the vertically transmissible gut microbiome of infants 3–7 days after birth, as well as enhanced horizontal transmission of potentially pathogenic species from the hospital environment. In dairy cattle, milk containing antibiotic residues is considered unsuitable for human consumption. However, this waste milk is often used to feed calves, making it possible for antibiotic-resistant microbial strains to establish in the underdeveloped GI tract of newborns by taking advantage of the limited competition for resources (Langford et al. 2003, Pereira et al. 2018). Finally, antimicrobial compounds can also impact microbial chemotaxis, with recent research showing that *P. aeruginosa* will migrate towards the source of antibiotics, all while releasing their own arsenal of bacteriocins and antibiotics (Oliveira et al. 2022). This is hypothesized to be a consequence of misdirected "competition signalling", with the bacteria mistaking the antibiotic for a competing bacterial colony and suicidally attacking it. Thus, not only can antibiotics kill beneficial microbes directly, but they can also compete with the chemoattractant strategies of hosts, further obstructing microbial recruitment.

In addition to the use of antibiotics, the increase in Caesarean section (C-section) deliveries and the decline of breastfeeding are important factors challenging the initial seeding and establishment of the microbiota in the human gut. Worldwide, C-section rates in humans are on the rise (Hoang et al. 2021). In Australia alone, ~37% of infants were born via C-section in 2020 (Australian Institute of Health and Welfare 2023). Infants delivered via C-section miss the opportunity to acquire maternal vaginal and faecal microbes, instead acquiring microbes from the hospital environment and mother's skin (e.g. *Klebsiella*, *Enterococcus*, and *Enterobacter*; Long et al. 2021). In contrast to infants delivered vaginally, those born via C-section exhibit a gut microbiota characterized by reduced levels of *Bifidobacterium* spp. and *Bacteroides* spp. However, opportunistic pathogens such as *Klebsiella* and *Enterococcus* are overrepresented (Reyman et al. 2019, Zhang et al. 2021b). The C-section-induced dysbiosis observed in early life is strongly associated with respiratory infections in the first year of life (Reyman et al. 2019) and several long-term health problems such as food allergies, asthma, diabetes, and obesity (Zhang et al. 2021a). To combat this, the seeding of C-section-born neonates with vaginal microbiota is gaining increasing attention as a therapeutic treatment (Mueller et al. 2023). Compounding the issue of C-section-induced dysbiosis, breastfeeding rates are declining (Breastfeeding Rate in Australia, Australian Breastfeeding Association). Although exclusive breastfeeding is recommended for the first 6 months of life (World Health Organization 2023), in some high-income countries, more than one in five babies are never breastfed (UNICEF 2018). Nonbreastfed infants have a distinctive microbiota profile compared to exclusively breastfed infants, with lower alpha-diversity (Ma et al. 2020), fewer *Bifidobacteria* and a higher relative abundance of opportunistic pathogens such as *Clostridioides difficile* (Pannaraj et al. 2017). A similar result regarding opportunistic pathogens was observed in ruminants since bottle-fed lambs showed higher levels of *Escherichia/Shigella* compared to suckled lambs (Bi et al. 2019). Supplementation of infant formula with probiotic strains, such as *Bifidobacterium longum* and *Lactobacillus rhamnosus*, has become a common practice (Braegger et al. 2011, Indrio et al. 2022). However, due to the heterogeneity of trial design and outcomes, no evidence currently supports the hypothesis that probiotic supplemented formula can effectively shift infant gut microbiota towards a desirable initial configuration (Indrio et al. 2022).

In cattle, mineral or methionine supplementation during gestation showed a positive effect on the calf microbiome, potentially limiting pathogen colonization (Elolimy et al. 2019, Hummel et al. 2021). In contrast, in ruminants, the low frequency of caesarean section (C-section) deliveries results in little concern regarding its implications to microbial recruitment in calves, although evidence suggests that the mode of delivery might influence the microbial profile in the preruminant phase (Cunningham et al. 2018) However, in comparison to human, in calf-feeding programs the use of waste milk (i.e. unsuitable for human consumption), milk replacers, and/or starter concentrate after colostrum feeding is common practice. Although the composition of some of these postcolostrum diets can negatively influence bacterial colonization, for example, by causing diarrhea in calves due to the presence of pathogenic bacteria in unpasteurized waste milk (Calderón-amor and Gallo 2020), different formulations of milk replacer diets also represent an opportunity for optimization of gut bacterial colonization. Administering probiotics to calves, such as dry yeast or compound probiotics containing multiple strains of live bacteria, can promote the establishment of beneficial gut microbiota, maintain microbiota stability, inhibit pathogen growth, and improve fermentation capacity (Du et al. 2023). However, the long-term effects of diet-influenced microbial colonization needs

to be evaluated, as differences due to starter diets might disappear in adult life, limiting the effects on adult performance (Dill-McFarland et al. 2019).

Microbial attachment to interfaces critical to One Health

Microbial attachment is fundamental to microbiome formation at interfaces, whether it occurs on soil particles (Mills 2003), roots (Wheatley and Poole 2018), or within hosts (Klemm and Schembri 2000). By attaching to interface surfaces, microorganisms can enhance their survival and colonization via biofilm formation (discussed in the section "Microbial interfaces critical to One Health"). In soil, plant root, and gut interfaces, a key benefit of attachment and biofilm formation is facilitating access to nutrients. Surfaces can attract nutrients by charge–charge or hydrophobic interactions, while other nutrients arrive passively via diffusion through aqueous environments (Beveridge et al. 1997). In the soil, attachment can also facilitate the transfer of electrons directly to surfaces (Nealson and Finkel 2011), minerals (Shi et al. 2016), or humic substances (Lovley et al. 1996). In the rumen, attachment to food particles is essential for microorganisms to efficiently breakdown complex plant cell walls and indigestible fibres to access nutrients (McAllister et al. 1994). In contrast, in the human gut, microbes attach to the outer mucus layer gaining access to mucins and mucin glycoproteins as a nutrient source. Furthermore, mucins play a complex role in mediating the spatial organization of gut microorganisms, thus impacting cooperation and cross-feeding interactions, and the transport of nutrients (Wang et al. 2021b).

In soils, attachment and biofilm formation can also help microorganisms evade or resist predatory pressures, for example from protists and nematodes (Matz and Kjelleberg 2005, Martins et al. 2022). In host-associated interface microbiomes, attachment processes can stimulate host immune responses which can offer the commensal community (as well as the host) protection from invading pathogens or predators (Weng and Walker 2013). For example, *Lactobacilli* and *Bifidobacteria*, which colonize the outer mucus layer in the human gut, are known to modulate the immune system. The varied mechanisms used to influence the immune system are yet to be fully characterized and ore research is required.

Attachment to surfaces is governed by fundamental physical, chemical, and biological processes (Muhammad et al. 2020) which explains the ubiquity of this behavioural phenomenon across microbial taxa and biomes. Universal binding forces (e.g. van der Waals forces, electrostatic forces, and hydrophobic interactions) underpin these processes (Berne et al. 2015). Initial, reversible attachment is mediated by environmental factors (Renner and Weibel 2011). Cell appendages (e.g. flagella, pili, and fimbriae) can be involved in this reversible attachment phase. More specific mechanisms, in particular surface proteins and extracellular polymeric substances (EPS), then facilitate irreversible attachment. The mechanisms can vary with species and environmental conditions of specific biomes. The transition between reversible and irreversible attachment is regulated by intracellular secondary messengers such as cAMP and c-di-GMP. These transduce environmental signals and trigger specific attachment processes including the production of cell appendages, surface proteins, and EPS (Toyofuku et al. 2016). Thus, it is ultimately the complex interplay between abiotic, biotic, and host factors that influences attachment of microbes in interface systems.

Abiotic factors impacting microbial attachment

Abiotic factors that influence microbial attachment can include chemical (e.g. pH levels, salinity, and the presence of specific ions), physical (e.g. surface area, roughness, pore spaces, fluid flow, and hydrophobicity) as well as environmental (temperature, oxygen availability, and moisture levels) conditions (De Weirdt and Van de Wiele 2015, Jiang et al. 2021). In the soil, for example, chemical influences such as ionic strength, pH (Palmer et al. 2007) and the physicochemical attributes of the substratum's surface including surface charge can impact the electrostatic and binding forces. These elements play a crucial role in fostering initial microbial attachment to particle surfaces (Carniello et al. 2018, Muhammad et al. 2020).

In interfaces such as soil and the rumen, particle size is a physical factor which influences attachment success. For soil ecosystems, particle size shapes the abundance and size of pore spaces, which can increase or decrease the number of available attachment sites and alter the availability of essential resources like water and nutrients (Griffin and Quail 1968, Hayashi et al. 2006, Goebel et al. 2011). In the rumen, the size of food particles influences their transit rate, and therefore, the time available for microbes to form attachments (Bowman and Firkins 1993). Consequently, perturbations or deliberate interventions that alter particle sizes are likely to influence attachment and subsequent microbiome composition in these systems. For instance, in the case of ruminants, altering the diet to modify food particle size and nutrient availability could change microbiome assembly. This, in turn, could result in functional changes like alterations to proportions of bacteria with the ability to break down substances such as cellulose or amylose (Bowman and Firkins 1993).

Finally, environmental features play a considerable role in attachment at interfaces and subsequent biofilm formation. It is noteworthy that certain host biomes, such as the plant rhizosphere and the human gut, exhibit both phylogenetic and functional parallels (Ramírez-Puebla et al. 2013). Both of these systems are open environments featuring large surface areas populated by microorganisms and in both, environmental factors such as gradients in oxygen and fluid shape the formation of distinct and diverse communities (Macfarlane et al. 2011, Mendes and Raaijmakers 2015).

Biotic factors impacting microbial attachment

Various biological mechanisms facilitate or inhibit attachment in diverse systems including soil particles, plant roots, the rumen, and human gut. Adhesins can aid attachment to both abiotic surfaces (Berne et al. 2015) including soil particles (DeFlaun et al. 1999) as well as biological surfaces, such as specific plant (Tomlinson and Fuqua 2009) and animal tissues (Kline et al. 2009, Chagnot et al. 2012, Donaldson et al. 2016). Some bacteria (e.g. lactobacilli) can bind to the mucus layer using specific adhesins, such as mucus-binding proteins, that recognize carbohydrate structures on the mucins (Etzold et al. 2014). Unlike symbiotic commensals that maintain a balance between mucin production and breakdown, pathogenic bacteria can secrete enzymes such as glycosidases and proteases, that break down the mucin polymers damaging the mucous layer to colonize deeper into the epithelial cells (Rogers et al. 2023). Many bacterial pathogens including *Vibrio cholerae*, *P. aeruginosa*, and *Salmonella enterica serovar* Typhimurium have Type VI secretion systems that are expressed during bacterial colonization and deliver various types of virulence factors, increasing pathogen fitness and facilitating adhesion to host cells (Hachani et al. 2016, Logan et al. 2018, Soria-

Bustos et al. 2020). Understanding the role adhesins play during attachment offers possibilities to alter colonization behaviour and select for desirable taxa (Pham et al. 2017).

Cellular appendages such as pili and flagella, normally associated with cell movement, also play a role in attachment. It was shown for *P. fluorescens* that increased piliation was positively correlated with both increased levels of hydrophobicity and attachment to corn roots (Vesper 1987). Interestingly, pandemic *V. cholerae* strains associated with cholera require the toxin coregulated pilus to colonize the gut and this adhesin is encoded by the filamentous CTX phage, highlighting the complexity of adhesion between the host and bacteria (Herrington et al. 1988). The involvement of flagella in attachment has been demonstrated for *A. brasilense* on wheat roots (Croes et al. 1993), and for *S. enterica* serovar Typhimurium on plant cell walls of fresh produce with implications for public health (Tan et al. 2016). In the rumen, there is a predominance of cellulolytic bacteria such as *Ruminococcus albus* and *Fibrobacter succinogenes*, which lack flagella or cilia (Miron et al. 2001). However, pilin-like appendages have been implicated in *R. albus* fibre adherence, together with glycocalyx and cellulosomes (Christopherson et al. 2014).

Other biotic factors, including competition for attachment sites, predation, and quorum sensing can also influence attachment. Different mechanisms of how plant-beneficial microorganisms can outcompete pathogens in the rhizosphere and on roots have been reviewed extensively (Wang et al. 2021c, Boro et al. 2022, Dow et al. 2023). However, attachment plays a critical role in this, which has been demonstrated for root colonization behaviour of *B. subtilis* leading to exclusion of *Escherichia coli* cells (Massalha et al. 2017). In the human gut, some bacteria such as *Bacteroides* spp., *Ruminococcus* spp., and *Bifidobacteria* spp. can metabolize complex, host-indigestible carbohydrates and degrade mucin, which can significantly impact attachment and colonization of other microbial species (Ventura et al. 2012, Wang et al. 2021d).

Host factors impacting microbial attachment

Furthermore, when considering host–microbiome interfaces, the genetic makeup of the host can influence mutual interactions between host and microorganisms, as well as host defence mechanisms, which can either facilitate or hinder microbial attachment. Host defences influencing attachment include physical barriers (e.g. cell walls or cuticles), or molecular components (e.g. pattern recognition receptors, antimicrobial peptides, and hormones). Host secretions, like mucus in the gut or root exudates, can provide a medium for microorganisms to attach (Swamy et al. 2016, Ruan et al. 2020), while secreted antimicrobial peptides may be inhibitory (e.g. for pathogenic microorganisms; Zong et al. 2020). In the human gut for example, the secretion of MUC2, as the main component of the mucus layer, influences bacterial attachment, while gene expression has been shown to be upregulated by specific probiotic strains (reviewed in Wu et al. 2020). Host immune responses include phagocytosis, the production of proinflammatory molecules, and the induction of adaptive immune responses, such as the production of T and B cells in humans (see the section "Impacts of microbial colonization to the host" for more details). These factors play a role in promoting attachment and maintaining beneficial microorganisms while limiting harmful pathogens (Hepworth et al. 2013, Doron et al. 2023).

Attachment is the first step towards colonization, community growth, and establishment of a functional microbiome that can interact with its host or environment. Interventions or perturbations during this early stage have the possibility of long term beneficial or adverse outcomes. Therefore, it is crucial that research continues to uncover the complex mechanisms mediating microbial attachment processes, including the precise molecular and metabolic signalling pathways and spatio-temporal relationships with physico-chemical and biotic factors including changes in the microhabitat environment.

Microbial growth, community development, and succession

Following attachment, microorganisms take advantage of the benefits available in their new microhabitat (outlined in the previous sections) and start growing and dividing to form microcolonies. Interestingly, different microbial taxa will often employ divergent growth strategies, even within the same genus. For example, Heydorn et al. (2000) showed that *P. aeruginosa* rapidly covered the substratum in a flat uniform biofilm, whereas *P. putida* initially formed microcolonies, then developed into 300 µm high cell clusters before transitioning to a filamentous form. Rapid proliferation and the ability to spread allows biofilm-forming microorganisms to occupy their target ecological niche, likely to the exclusion of competitors. Furthermore, biofilm thickness and substratum coverage are influenced by nutrient availability, such as for *P. aureofaciens*, where a positive correlation has been found with higher concentrations of the added electron donor citrate (Heydorn et al. 2000), while biofilm formation was enhanced when higher concentrations of nutrients were supplied to soil (Wu et al. 2019). On plant roots, colonization and initial growth of *B. subtilis* were observed just above the growing *Arabidopsis thaliana* (Arabidopsis) root tip, which subsequently led to biofilm formation elsewhere along the whole root and exclusion of other bacteria (Massalha et al. 2017). This may be related to substrate stiffness which impacts early biofilm formation by modulating twitching motility in *Pseudomonas* (Gomez et al. 2023).

In nature, most biofilms are composed of several species of microorganisms. This extends the genetic and metabolic capabilities of the biofilm as a habitat and allows interspecies collaboration (e.g. syntrophy; Sadiq et al. 2021). In the rumen, for example, syntrophic bacteria and archaea are positioned within the biofilm based on attraction to gradients of their preferred substrates (Leng 2017). Additionally, fungi within the biofilm, often located within plant material, contribute to its degradation process (Leng 2017). In the rumen, biofilm formation ensures the continuous presence of the microbial community on ingested plant particles despite the vigorous mixing and rumination, allowing for sustained degradation of the feed that would otherwise be indigestible to the animal. In humans, multispecies biofilms have been found in various parts of the human body, such as the oral cavity (Anderson et al. 2020) and the appendix (Palestrant et al. 2004) or, similar to the rumen, attached to food particles (Macfarlane and Macfarlane 2006). However, their existence on mucosal surfaces is still under debate and bacteria often occur as aggregates or microcolonies rather than fully developed biofilms (Tytgat et al. 2019). However, biofilm formation by pathogens can lead to disease in the human gut. For example, biofilms dominated by *Bacteroides fragilis* and *Fusobacterium nucleatum* are associated with increased incidence of inflammatory bowel disease and colorectal cancer (Tytgat et al. 2019).

The benefits of growth on surfaces and biofilm formation are conveyed by the produced matrix of EPSs. This matrix provides habitat diversity, helps capture resources and enhances resistance against antimicrobials and toxic metals (Flemming et al. 2016).

However, the structure, size, and composition of the matrix influence the interactions between members of the biofilm and enable microenvironments (niches), and thus heterogeneity to emerge (Gordon et al. 2019). For example, biofilms attached to the rumen epithelium differ in terms of microbial diversity and community structure compared to the bacterial communities attached to feed particles (De Mulder et al. 2016). It is expected that different niches within the rumen exhibit specific microbial characteristics based on the resident microorganisms as well as the chemical composition of the ingested feed (Liu et al. 2016). Other factors shaping the growth and dynamics of microbial communities in terms of competition and cooperation are cross-feeding and the production of various microbial substances such as quorum sensing (QS) signals, bacteriocins, hydrogen peroxide, and lactic acid (Wu et al. 2019, Ruan et al. 2020). By secreting these substances, bacteria can influence biofilm formation and microcolonization by other microbiomes, as well as their growth and development. For example, autoinducer-2, a QS signal that regulates the behaviour of bacteria, increased the abundance of Firmicutes in the gut in a mouse model study (Thompson et al. 2015), promoted root colonization of beneficial rhizobacteria, *Bacillus velezensis*, in plants (Xiong et al. 2020), and was shown to be an abundant QS mechanism in the rumen (Won et al. 2020). Faust et al. (2012) reported significant co-occurrence and coexclusion relationships in the human microbiome both within and between body sites and showed the competition between dominant commensal taxa such as *Prevotellaceae* and *Bacteroides* in the gut and co-occurrence of some pathogens like *Treponema* and *Prevotella* in the dental plaque.

Mechanisms of growth, community development, and succession

Growth and biofilm formation generally continues unabated until adverse effects occur, some of which are elicited as a consequence of growth, such as nutrient or oxygen limitation or negative interactions with other microbes (Rendueles and Ghigo 2015) or the host (Rudrappa et al. 2008, Watters et al. 2016). For example, oxygen limitation has been shown to induce dispersal from the biofilm (Thormann et al. 2005) or can select for the subsequent growth and succession of anaerobes. Biofilms in soils influence the movement of water and air as their EPS was documented to fill pores of more than 50 µm in size (Hand et al. 2008). The change from aerobic to anaerobic metabolism can cause acidification of the local milieu and have consequences on the viability of different members of the biofilm microbiome (Flemming et al. 2016).

Predation by protists and bacteriophages play an important role in the growth, community assembly, and succession of microbial communities with functional significance and overall biofilm dynamics at interfaces (Böhme et al. 2009, Hungate et al. 2021). Protozoan feeding shapes microbiome assembly in the rhizosphere (Gao et al. 2019), rumen (Williams et al. 2020, Solomon et al. 2022), and human gut (Chabé et al. 2017). Similarly, phages also control the size and composition of these microbiomes (Koskella and Taylor 2018, Gilbert et al. 2020, Holtappels et al. 2023). The mechanisms of predation, be it via protozoan grazing or lysis by phages, represent an understudied but promising intervention tool to elicit benefits for the host including nutrient supply (Gao et al. 2019, Gilbert et al. 2020) or biocontrol of pathogens (Chabé et al. 2017, Baliyan et al. 2022, Holtappels et al. 2023).

Growth, community development, and succession at soil and plant root surfaces

Early growth of soil bacteria and their capacity to form biofilms on surfaces was studied by Burmølle et al. (2007) using a biofilm flow model. They showed that *B. circulans* was an early colonizer persisting, however, only for 1 day. It was succeeded by several *Pseudomonas* strains that in turn were outcompeted by *Dyadobacter fermentans* after 7 days. Both *B. circulans* and *D. fermentans* were characterized as monospecies biofilm formers given their dominance in the biofilm community at certain timepoints. Interestingly, only one of the *Pseudomonas* strains was classified as a biofilm former. This trait was enhanced when it was grown in a multispecies biofilm with a *Chryseobacterium* strain suggesting that cooperation between the two strains lead to stronger biofilm formation than each strain exhibited on their own. In an experiment with artificial soil (Wu et al. 2019) biofilm formation increased microbial diversity, evenness, and metabolic activity.

Successional patterns of rhizosphere communities are influenced by plant development and growth stages (Ajilogba et al. 2022), climatic conditions (Durán et al. 2022), root exudates (Kawasaki et al. 2021, Durán et al. 2022), root binding site (Donn et al. 2015), and soil type (Qiao et al. 2017). Chaparro et al. (2014) reported that rhizosphere communities (specifically Acidobacteria, Actinobacteria, and Bacteroidetes) associated with the model plant Arabidopsis at the seedling stage differed significantly from other developmental stages, e.g. vegetation, growth, and flowering. However, it is not clear how these communities change after plants senesce and begin a new growing season. In the common annual grass *Avena fatua*, rhizosphere bacterial communities followed consistent patterns across two growing seasons, even though the initial communities were different (Shi et al. 2015). For example, the relative abundance of Alpha-, Betaproteobacteria, and Bacteroidetes increased as the relative abundance of Acidobacteria, Actinobacteria, and Firmicutes decreased. Seasonal differences (temperature, photoperiod, and light intensity) between northern and southern Europe strongly influenced adaptive differentiation between two Arabidopsis populations, while differences in soil factors only had a weak effect. In contrast, subterranean differences in soil properties were more important than climatic differences in differentiating rhizosphere microbiomes (Durán et al. 2022). Strategies to enrich certain microbiomes, such as through the application of probiotic consortia (Zhang et al. 2020) to seeds, led to reorganization of the associated microbiome (Zhang et al. 2019). For example, pepper seedlings treated with *B. velezensis* resulted in changes in the composition of the rhizosphere microbiome during two seasons in field experiments (Zhang et al. 2019). Similarly, the nodule endophyte *Agrobacterium* sp. 10-C2 affected the richness and structure of the common bean rhizosphere bacterial communities (Adeleke et al. 2022). Microbiome succession in the rhizosphere and rhizoplane environments is also influenced by the presence of fungal pathogens. For example, specific disease suppressive endophytic root microbiomes were activated in the presence of *Rhizoctonia solani* (Carrión et al. 2019). During root rot disease in Avocado, *Phytophtora* increased the relative proportion of *Pseudomonas* and *Burkhoderiales*, while the abundance of other fungal opportunistic pathogens also changed (Solís-García et al. 2021). These examples highlight that the stability and succession of some microbial consortia can be influenced by the presence of certain microbial species.

Although rhizosphere microbiomes differ from those of the surrounding soil, little is known about how these root-associated mi-

crobial communities are developed or stabilized over growing seasons. Rhizosphere succession was characterized by a significant reduction in both taxonomic and phylogenetic diversity accompanied by decrease in both richness and evenness compared to background soil communities (Shi et al. 2015). Growth and development of rhizosphere microbiomes is driven by various factors and challenges. Nutrient availability in the soil is one of the limiting factors for the enrichment of certain members of the microbiome. Plant exudates provide the carbon source for the microbiome and influence their functional activity and diversity. However, many microbes cannot thrive on plant exudates alone and presumably also require additional nutrients from the soil (Tkacz et al. 2015). Soil pH is another key factor that can challenge the successful establishment of microbial communities, with endosphere, rhizosphere, and bulk soil and endosphere microbial communities showing different tolerances to pH ranges (Fierer and Jackson 2006). Alkaline soil pH affects bulk soil, rhizosphere, and root endosphere microbiomes of plants growing in a Sandhills ecosystem (Lopes et al. 2021). Both the developmental age of plants and abiotic factors (e.g. soil type and chemistry, climate) exert a strong selective force on the composition of rhizosphere microbial community. In contrast, timing of soil exposure was more important for shaping the root microbiome composition at maturity than plant age and soil related factors (Aleklett et al. 2022).

Growth, community development, and succession in the rumen

Rumen development starts with a nonrumination phase in the first weeks after birth when animals feed almost exclusively on liquid feed, then moves to a transition phase where small quantities of solid feed are ingested, reaching the final rumination phase around 8 weeks after birth concomitant with the increase of solid feed (Yáñez-Ruiz et al. 2015). Ruminal bacterial colonization reflects those phases, starting with Proteobacteria and Firmicutes acquired from the dam's vaginal canal, saliva, and milk, as well as from the environment, which switch from aerobic or facultative aerobic to strictly anaerobic communities. This process results in Proteobacteria being replaced by Bacteroidetes, which includes genera capable of using components in milk (*Bacteroides*) and some commonly found in mature ruminants (*Prevotella* and *Ruminococcus*). Finally, Bacteroidetes and Firmicutes become the dominant phyla with an increase of genera capable of utilizing starch and fibre from solid feed, such as *Prevotella* and *Ruminococcus* (Li et al. 2023). Although both phyla are present across various microenvironments within the adult rumen, Firmicutes (particularly *Clostridiales*, *Lachnospiraceae*, *Mogibacteriaceae*, *Christenellaceae*, and *Erysipelotrichaceae*) are more abundant in fluid communities, whereas Bacteroidetes (specifically *Muribaculaceae* and *Prevotellaceae*) are predominant in mucosa-associated communities (Pinnell et al. 2022). Early in life, the rumen is also colonized by methanogenic archaea. Not much is known about their viability and metabolic activity during the first stages of rumen development when, without solid food, archaea depend on bacteria such as *Geobacter* spp. and *Ruminococcus flavefaciens* for essential hydrogen and electrons for methanogenesis (Guzman et al. 2015). However, methanogenic archaea are unevenly distributed into the four rumen factions (solid-fraction, liquid-fraction, protozoa-associated, and epithelium-associated) with higher presence in the liquid fraction and relative abundances being influenced by age, diet, and weaning (Wang et al. 2017a, Pinnell et al. 2022). Anaerobic fungi also seem to establish quickly after birth and go through different phases before reaching stability as more solid food is ingested (Yin et al. 2022). Ciliate and flagellate protozoa appear later in the development, around 15 days after birth, and are transferred from animal to animal through saliva (Li et al. 2023). Therefore, the first weeks of a ruminant's life provide a window of opportunity to influence microbial colonization in the rumen to support better feed utilization, decrease methane production and optimize overall health (Yáñez-Ruiz et al. 2015, Huuki et al. 2022).

Different types of feed and dietary changes can affect the ruminal microbial population and its ability to efficiently degrade specific feed components. High-grain diets or sudden dietary changes can lead to a decrease in ruminal pH, causing acidosis. Subacute rumen acidosis (SARA) is a highly prevalent disease in dairy cows that can lead to breakdown of the rumen epithelial barrier resulting in increased circulating lipopolysaccharide (LPS), a marker of bacterial translocation (Krogstad and Bradford 2023). SARA-susceptible cows were shown to have a higher proportion of starch-degrading bacteria (e.g. *Prevotella*) in relation to fibre-degrading bacteria (e.g. *Ruminococcaceae*, *Ruminococcus*, and *Papillibacterin*) in their rumen causing an increased production of VFAs which, in excess, can disrupt metabolic homeostasis (Zhang et al. 2022). The influence of SARA in other areas of the animal is currently being investigated, including hindgut dysbiosis induced by a reduced faecal pH (Neubauer et al. 2020, Krogstad and Bradford 2023) and mastitis, possibly due to increased presence of Proteobacteria in the rumen (e.g. *Stenotrophomonas*) and circulating LPS (Hu et al. 2022, Zhao et al. 2022a). Other factors that can be detrimental to microbial population due to changes in ruminal pH or decrease in feed intake include environmental stressors, such as heat stress (Kim et al. 2022), animal transportation (Li et al. 2019), or changes in management practices (Sanjorjo et al. 2023) which can, for example, favour the growth of lactate-producing bacteria such as *Streptococcus*, *Enterobacteriaceae*, and *Lactobacillus*. In addition, feed ingredients or plants containing natural toxins can have unintended consequences on ruminal microbial development, leading to imbalances in the rumen microbiota (Loh et al. 2020). These imbalances or sudden shifts in the ruminal environment can adversely affect the microbial community, leading to a decline in rumen health and fermentation efficiency.

Growth, community development, and succession in the human gut

In the early stages of human development, the microbiota is generally low in diversity and, during the first few years of life, undergoes a series of transitions gradually evolving towards a more complex, adult-like composition (Tamburini et al. 2016). Three main phases occur including the development phase (3–14 months) characterized by a low-diversity microbiota including Actinobacteria, the transitional phase (15–30 months), and the stable phase (older than 31 months) with significantly higher diversity and richness (Stewart et al. 2018, Vatanen et al. 2018). As an infant begins to consume breast milk and solid food the microbiome becomes more diverse and dominated by obligate anaerobic bacteria, such as Bifidobacteria and Lactobacilli (Milani et al. 2017), which are specialized in breaking down complex sugars in milk and other food. Many studies showed that by the age of 2.5 years, when solid food has become the main component of the diet, the microbiome composition stabilizes and resembles the adult microbiota mainly composed of Firmicutes and Bacteroidetes (Stewart et al. 2018, Ahearn-Ford et al. 2022). Changes

in this composition are driven by strong deterministic processes (Bäckhed et al. 2015) and factors such as age, geographical location, host, genetics, diet, immune system development, exposure to chemicals, and the initial colonizers' founder effects (Donaldson et al. 2016). However, founder colonizers and diet are suggested to have the greatest impact on the establishment of microbial communities in the long term due to the syntrophic interactions (Conlon and Bird 2014) as shown when comparing the microbiomes of the Hadza hunter–gatherers with people on a western diet (Fragiadakis et al. 2019). The early microbiome provides important benefits, such as training the immune system, producing vitamins and other nutrients, and regulating metabolism. Martín-Peláez et al. (2022) showed in a recent systematic review that the use of prebiotics and probiotics such as *Lactobacillus*, *Bifidobacterium*, *Propionibacterium*, and *Streptococcus* during pregnancy and lactation have positive impacts on the development of the gut microbiota of C-sectioned newborns, especially regarding *Bifidobacterium* colonization (Martín-Peláez et al. 2022). Beneficial bacteria can also be introduced into the gut through probiotic supplements and fermented foods. The effects of probiotics in inhibiting potential pathogens and supporting a healthy gut microbiota has been widely accepted (Hill et al. 2014), although the efficacy of probiotics varies depending on the specific strains, doses and formulations. Additionally, the viability and stability of probiotic strains are crucial to ensure a successful probiotic recruitment into the human gut, where they can confer health benefits (Wendel 2022).

The human GI tract poses several challenges for the growth and development of gut microbiota as microcolonies. Some of these challenges are: the low pH of the stomach and duodenum, the presence of bile acids in the small intestine, the thick and fast-shedding mucus layer that covers the intestinal epithelium, the high turnover rate of epithelial cells, the mechanical stress from the movement of intestinal fluid and stool and the presence of antimicrobial agents produced by the host or other microbes (Ruan et al. 2020, Arias and Brito 2021). Some bacteria establish better in the human gut and dominate the community because they have adapted to the specific environmental conditions and interactions with other microbes and the host. For example, *Lactobacillus*, *Streptococcus*, *Staphylococcus*, and *Enterobacteriaceae* are the main bacteria in the stomach because they can persist in this environment of high acidity and enzymatic activity. Moreover, the presence of *Helicobacter pylori* may affect the diversity and microbiome composition of the stomach and lower GI tract (Dash et al. 2019, Ye et al. 2020). In adults, while *Lactobacillaceae* and *Enterobacteriaceae* are the dominant families in the small intestine because they can grow quickly in the presence of bile acids, the microbiome in the colon is highly enriched and diverse and dominated by *Bacteroidaceae*, *Prevotellaceae*, *Rikenellaceae*, *Lachnospiraceae*, and *Ruminococcaceae* enabling the fermentation of complex carbohydrates from foods and fibres that have not been digested (Derrien and van Hylckama Vlieg 2015, Ruan et al. 2020). Moreover, the small intestine has higher oxygen and nutrient concentrations than the colon, which favours aerobic or facultative anaerobic bacteria. In contrast, the colon is mostly anaerobic with complex carbohydrates and lower oxygen levels and thus supports the growth of obligate anaerobic bacteria that produce SCFAs and micronutrients (Conlon and Bird 2014, Kastl et al. 2020, Ruan et al. 2020).

Overall, growth, biofilm formation, and succession encompass a myriad of complex microbe–microbe and microbe–host interactions, which can result in beneficial or detrimental outcomes for the organisms involved. While some of the effects of establishing biofilms were already touched on in this section, they will be more critically evaluated below.

Impacts of microbial colonization to the host

Thus far, we have discussed the underlying mechanistic principals that shape microbiome assembly at interfaces across a range of biome/ecosystem boundaries. These processes lead to the formation of microbial communities with emergent functional properties that can reciprocally shape host phenotype and health. Associations between microbiomes and a range of host traits have been described, including developmental trajectories (Dominguez-Bello et al. 2019), immunity (Tripathi et al. 2018), longevity (He et al. 2022), and even behaviour, such as feeding and mating preferences (Sharon et al. 2010, Ezenwa et al. 2012) as well as fear-response in prey species (Boillat et al. 2020). Thus, microbiomes impact the adaptive evolution of their hosts as both selective forces, and modalities of host adaptation to environmental pressures (Kolodny et al. 2020). For example, host evolution may be influenced by the presence of gut microbiota that expand a host's dietary niche (Moran et al. 2019), or provide it with essential limiting nutrients (Salem et al. 2014). There is also evidence that imperfect vertical transmission of microbiota is selected for in unstable environments (e.g. variable extremes in climate or fluctuating resource availability), as it enhances microbiome variation and thus the phenotypic adaptability of host populations (Bruijning et al. 2022). To understand these complex associations, research has begun to focus on microbiome-wide association studies that link microbial community structure and function to host phenotypes (Gilbert et al. 2016, Awany et al. 2019). Such studies have also begun incorporating microbiome features (e.g. taxonomy or microbial genomes) into genome-wide association studies to explore the mechanisms by which microbiomes mediate the translation of host genotype into phenotype (Tiezzi et al. 2021).

Host nutrition

Microbiomes play crucial roles in enhancing host nutrition across the key microsites discussed in this review, primarily in the form of enzymatic transformation of unavailable resources (e.g. recalcitrant food items and soil organic matter) and the biosynthesis of essential nutrients and vitamins. In the rhizosphere, bacteria and fungi enhance the bioavailability of limiting nutrients, such as nitrogen, phosphorus, and ferric iron, via mineralization, acidification, and the production of scavenging compounds (e.g. siderophores; Masood and Bano 2016). Specialist fungi and bacteria take this process further, forming intimate symbiotic associations with plant roots that have arisen independently several times throughout plant evolution. For example, current estimates suggest that 40 000–50 000 fungal species can form mycorrhiza with plant hosts (van der Heijden et al. 2015), effectively extending the range of the root system and enhancing the uptake of phosphorus, nitrogen, and water. Similarly, diazotrophs, both symbiotic (*Rhizobium* and *Frankia)* and nonsymbiotic (e.g. *Azospirillum* and *Azotobacter)*, have the enzymatic machinery required to generate ammonia by atmospheric nitrogen fixation, contributing to their host nutrition in return for energy-rich carbohydrates. The root microbiome also influences the plant's innate ability to absorb and utilize essential nutrients by altering the expression of the host transcriptome to enhance nutrient transport and metabolism (Castrillo et al. 2017). For example, using a collection of synthetic communities (SynComs; Wang et al. 2021a) demonstrated that the root microbiome of soybean could enhance phosphate uptake of the host by triggering plant systemic phosphate starvation signalling cascades. In the rumen of livestock, the resident microbiome expands the host's enzymatic repertoire

to enable the hydrolysation of complex cellulosic materials, which form the core of their diet, into simpler compounds like VFAs. These are central energy sources for ruminants, with recent findings suggesting that ∼70% of the energy content of plant polysaccharides is maintained and delivered to the host in this form (Russell et al. 2009). The procedural breakdown of complex plant matter in the rumen is highly coordinated, as the metabolic products of specific taxa serve as substrates for subsequent catabolic reactions by different microbes (Xu et al. 2021). The rumen microbiome also plays a role in nitrogen metabolism, converting vegetal proteins into microbial proteins that can be utilized by the host and its microbiome for growth and cellular maintenance. The evolutionary contract between ruminants and their microbiome has resulted in complete reliance, such that the loss of the metabolic functions of the rumen microbiome would rapidly result in starvation and death. This absolute level of dependence on gut microbiota for nutrition can also be found in certain insect species (e.g. termites) and phytoplankton. In the human gut, the microbiome's contribution to nutrition is more peripheral. In common with the rumen microbiome, the human gut microbiota break down complex carbohydrates, such as dietary fibre, that are resistant to digestion by human enzymes. The resulting SCFAs serve as energy sources for the cells lining the colon and are involved in regulating various physiological and immunological processes. Crucially, as in the rumen, the human gut microbiota is responsible for the production of essential micronutrients, such as B-group vitamins, which serve as precursors of indispensable metabolic cofactors (Rodionov et al. 2019).

Host immune function

The most extensively studied connections between microbiomes and host phenotypes relate to the profound effects the microbiome exerts on various aspects of host immunity via direct and indirect means, such as antibiosis with pathogens, colonization resistance, defensive priming of host immunity, and maintenance of immune homeostasis (Santhanam et al. 2015, Ritpitakphong et al. 2016). For example, microbiomes of the human gut (Rea et al. 2011), livestock rumen (Shi et al. 2023), and plant root (Hol et al. 2015) have been shown to directly inhibit pathogen proliferation through the production of an assortment of antimicrobial compounds. The target specificity of these compounds ranges from those with high precision e.g. bacteriocins, which primarily target closely related or competing bacterial strains; through to kingdom-spanning bioactives e.g. gramicidins, which have been shown to exhibit antibiotic (Weinstein et al. 1980), antifungal (Kondejewski et al. 1996), and antiviral (Enayathullah et al. 2022) activities. Microbiomes can also indirectly promote resistance to pathogens by defensively priming the host's immune system. For example, the proliferation of Bacteroidetes in the postweaned gut of mice have been shown to prime the production of intestinal interleukin (IL)-36, which elicits macrophage-dependent protection against the pathogen *Klebsiella pneumoniae* (Sequeira et al. 2020). In animals, these processes are largely mediated by the gut-associated lymphoid tissue, which is a sprawling immune organ associated with the intestine and thus frequently exposed to foreign antigens. Immunomodulatory compounds produced by the gut microbiome (e.g. SCFAs, tryptophan derivatives, and LPS) play essential roles in this process. For example, SCFA produced via the microbial fermentation of dietary fibre stimulates the synthesis of anti-inflammatory cytokines, while derivatives of tryptophan catabolized by intestinal bacteria such as indole, indole acetic acid, and kynurenine are modulators of the aryl hydrocarbon receptor pathway, which regulates natural killer T-cell levels and moderates inflammatory responses (Ghiboub et al. 2020).

Similarly, compounds produced by the root microbiome aid in the maturation of the plant's innate immune system, facilitating both local tolerance to beneficial microbes and priming plant immunity via induced systemic resistance (ISR), enabling the plant to respond more rapidly and with greater intensity to pathogen infection. The method of ISR induction, mediated by the phytohormones jasmonic acid and ethylene signaling pathways is surprisingly distinct from that of pathogen induced stress responses, which primarily develops via signaling cascades involving salicylic acid (Pieterse et al. 1998). Mycorrhizal fungi have been shown to enable root colonization through the suppression of localized plant defence signalling, mediated by the delivery of small, secreted effector proteins into the host root (Plett et al. 2014) while also enhancing the levels of plant-produced compounds associated with pathogen defence, such as phytoalexins (Yao et al. 2003) and hydrolytic enzymes (chitinases and glucanases; Pozo et al. 2002). There is extensive literature discussing rhizobacterial-mediated ISR, particularly among bacteria belonging to the genera *Pseudomonas*, *Bacillus*, and *Serratia*. The large genomes of these bacteria endow them with a large repertoire of signalling molecules and phytohormones, with which they influence plant development and defense processes (Abdelaal et al. 2021). For example, VOCs released by several root-associated *Bacillus* were shown to trigger an ethylene-dependent ISR in Arabidopsis seedlings, which significantly reduced their disease severity upon infection with the pathogen *Erwinia carotovora* (Ryu et al. 2004). Similarly, the rhizobacteria *P. fluorescens* was shown to trigger systemic resistance in Arabidopsis against several pathogens and insect herbivores by priming leaf expression of jasmonic acid-responsive genes (Pozo et al. 2008). The impact of beneficial root microbes on plant health is not restricted to biotic interactions, as they have also been shown to alleviate a plethora of abiotic stress conditions (Dimkpa et al. 2009), including but not limited to salinity (Nadeem et al. 2007), drought (Yuwono et al. 2005), and heavy metal toxicity (Xiao et al. 2021).

The influence microbiomes exert on host immunity is not restricted to localized interactions, as many sophisticated signalling mechanisms bridge distant tissues and organs to elicit systemic responses in host immunity. For example, the gut–brain axis bridges the gut microbiome, the enteric nervous system of the gut, and the central nervous system. As a consequence of multisystem involvement, the gut–brian axis plays a crucial role in the production and regulation of neurotransmitters, such as serotonin, dopamine, and gamma-aminobutyric acid, which are essential for mood regulation and cognitive processes. These metabolites travel via portal circulation, where they can impact the local neuronal cells of the enteric nervous system, as well as the afferent pathways of the vagus nerve, establishing direct signalling with the brain. Intestinal bacteria such as *Bacteroides*, *Parabacteroides*, *Lactobacillus*, *Bifidobacterium*, and *Escherichia* spp. produce gamma-aminobutyric acid, the primary inhibitory neurotransmitter (Barrett et al. 2012, Strandwitz et al. 2019). Similarly, microbially produced indoles have been shown to impact brain function, behaviour, and aging (Jaglin et al. 2018). This recent research has triggered a paradigm shift in our understanding of neurological disorders, revealing a previously underappreciated link between the microbiome and the brain. Recent reports have implicated dysbiosis of gut microbiota in neurological and neurodegenerative disorders such as anxiety, depression, Parkinson's disease, Alzheimer's disease, and autism spectrum disorder (Morais et al.

2021). In patients with Parkinson's disease for example, reduced levels of butyrate, propionate and acetate have also been reported (Aho et al. 2021), while toll-like receptor 4-mediated intestinal dysfunction triggered by microbiome-derived LPS has been shown to contribute to intestinal and central nervous system inflammation (Perez-Pardo et al. 2019).

Similar organism-spanning mechanisms of microbial interaction have also been shown in plants. During plant infection, microbial-derived small RNAs (sRNAs) have been demonstrated to migrate between the pathogen and the host, remotely altering the plant's immune response through RNA interference (Weiberg et al. 2013, Regmi et al. 2021). For example, sRNAs of the fungal pathogen *Botrytis cinera* were shown to translocate into Arabidopsis and tomato cells and downregulate plant defence-related genes, such as transcription factors, receptor like-kinases, and cell wall modifying enzymes; promoting host diseases susceptibility (Weiberg et al. 2013, Wang et al. 2017b). Similarly, in head blight disease in wheat, the pathogenic fungus *Fusarium graminearum* was shown to utilize sRNAs to silence the resistance-related gene Chitin Elicitor Binding Protein (Jian and Liang 2019). These remote means of modulation are not limited to host–pathogen interactions, as rhizobial tRNA-derived sRNAs have been shown to regulate host nodulation (Ren et al. 2019), while *in silico* analysis has provided evidence for the involvement of cross-kingdom RNA interference in the arbuscular mycorrhizal association between *Gigaspora margarita* and its plant host (Silvestri et al. 2020). There is growing evidence that analogous signalling pathways are also present between pathogenic bacteria and human hosts. For example, *Legionella pneumophila* (Sahr et al. 2022) and *P. aeruginosa* (Koeppen et al. 2016) have been found to excrete sRNAs via outer membrane vesicles that mimic host microRNAs and act to repress host immune defence signalling pathways. The remarkable capacity of microbial sRNAs to modulate host gene expression and phenotypic outcomes creates new and exciting avenues for agricultural and therapeutic interventions, highlighting the potential for microbiome-based alternatives to conventional agrichemicals and antibiotics, in the prevention and treatment of globally significant diseases in crops, livestock, and humans.

Influence of the soil microbiome on human, animal, plant, and environmental health

The global soil microbiome is an abundant reservoir of microbial diversity and function, the characteristics of which have both near and far-reaching impacts on environmental and biological systems. Here, we highlight how soil microbiome features and processes mediate impacts on the global environment and biotic hosts, reinforcing the utility of a One Health, systems biology approach to all microbiome science.

Soil microbiomes directly influence soil features and processes such as soil acidity, carbon sequestration, nutrient cycling (production and consumption of various mineral and organic forms of carbon, nitrogen, phosphorus, sulfur, iron, and so on), pathogen suppression and degradation or transformation of xenobiotic compounds and heavy metals (Fierer 2017). These phenomena have a number of large-scale indirect effects on biological hosts. For example, the role of soil microbiomes in carbon sequestration has global consequences for all ecosystems and organisms due to its role in mitigating climate change (Bhattacharyya et al. 2022). Carbon use efficiency of a microbial community is critically important to promoting soil carbon storage globally, highlighting the importance of soil microbiomes on a planetary scale (Tao et al. 2023). Similarly, soil microbiome biodegradation and transformation of toxic compounds impacts plant productivity, water quality, and ecosystem services and thereby indirectly influences global human and animal health (Singh et al. 2023).

Grazing behaviour of ruminants, such as sheep and cows, often leads to the direct consumption of soil and plant-associated microbes (Banerjee and van der Heijden 2023). A proportion of these microbes may colonize the rumen microbiome and contribute to the breakdown of recalcitrant plant matter, though little is known about the contribution of soil- and plant-borne organisms to this process, relative to the native rumen microbiome (Attwood et al. 2019). Pathogens may also be transmitted from soil and plants consumed by ruminants. For example, survival and transmission of *Bacillus anthracis*, the aetiological agent of anthrax, is thought to be influenced by both soil communities and its interactions with plant matter highlighting the interconnectedness of soil, plant, and animal microbiomes (Ganz et al. 2014).

Soil microbiomes may impact humans in several ways. The continuum from soil to plant to food being a key pathway for this influence. On this continuum, the soil microbiome impacts humans via its influence on the nutritional quality of the plants we consume (Banerjee and van der Heijden 2023). Additionally, soil-derived plant-associated organisms that are consumed may have beneficial or detrimental effects. For example, soil microbial diversity has an inverse relationship with the survival of *E. coli* O157:H7, an enteropathogen that often causes large-scale outbreaks of GI disease via contamination of produce—indicating soil biodiversity may control transmission of certain human pathogens (van Elsas et al. 2011). Furthermore, soil-derived plant-borne organisms can carry antimicrobial resistance genes, which may lead to increased gut carriage of drug resistant commensals and opportunistic pathogens, increasing the risk of mortality or fatality if infection occurs (Brinkac et al. 2017).

The diversity and composition of soil microbiomes, along with the functions performed by specific microbial species, have been linked to various effects on environmental, human, and animal well-being as part of interconnected microbiomes. To translate an understanding of microbiomes into improved health and environmental outcomes, it is important to fully comprehend these relationships, identify the drivers for functional benefit, and effectively address the challenges posed by global change. To achieve this, it is necessary to employ systems biology approaches that can uncover underlying mechanisms, enable accurate predictions, and facilitate targeted interventions. Such comprehensive understanding and conservation efforts are essential to elevate our knowledge and response to the profound transformations occurring worldwide.

Approaches for microbiological research for the study of microbiome interactions

Current and emergent technologies provide an ever-expanding toolkit with the potential to address outstanding questions regarding microbiome development, function, and interactions in unprecedented detail. Genomics, transcriptomics, proteomics, metabolomics, and meta-variants thereof, theoretically allow researchers to access the full spectrum of the molecular biology of a microorganism or microbial community and integrate these observations with the abiotic chemistry of a given ecology. Advances in instrumentation for these approaches are supported by novel analytical methods capable of integrating various 'omics data combinations such as factor analysis, network analysis, metabolic modelling, and machine-learning methods. Imaging technology

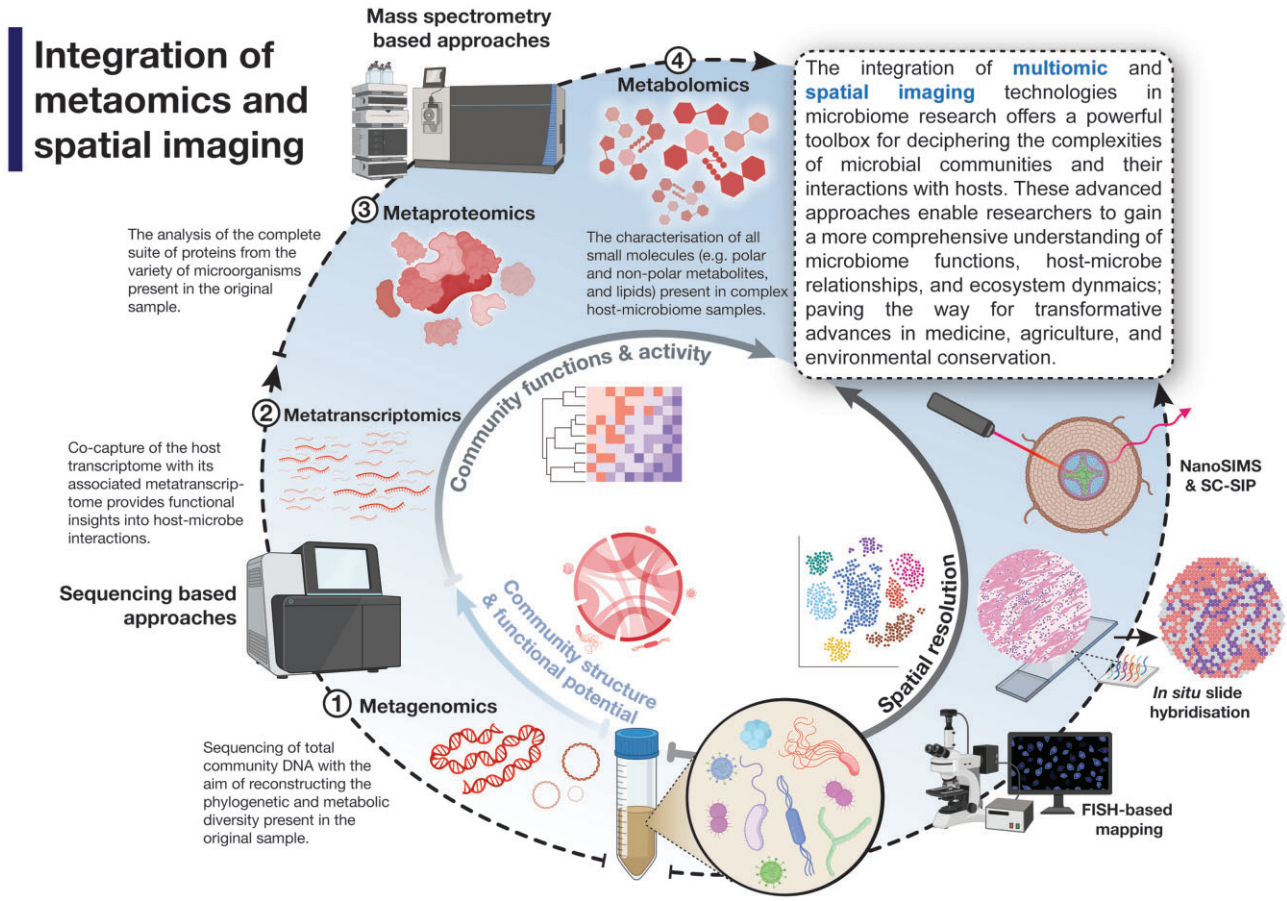

Figure 2. Illustration of the techniques and tools available to study the taxonomic composition, functions, and interactions of microbiomes with hosts and the environment. The four primary technologies used to characterize the major biopolymer classes (DNA, RNA, amino acids, and metabolites) in complex microbiome samples (left side of diagram) have been defined as *sequencing based* e.g. metagenomics and metatranscriptomics; and *mass spectrometry based* e.g. metaproteomics and metabolomics. Coinciding with this progression of approaches, these techniques provide insights into microbial community composition and functional potential, through to the characterization of community functions and interactions with the host. On the right side of the diagram, emerging technologies utilizing specific DNA sequence-based labelling (FISH) and isotopically enriched molecule probing (SIP) tools provide insights into the spatial distribution of microbial communities and their functionality *in vitro* and *in vivo*. FISH—fluorescence in situ hybridization; SC-SIP—single cell stable isotope probing; and NanoSIMS—nanoscale secondary ion mass spectrometry.

provides the opportunity to contextualize such molecular observations in physical space, a dimension that is typically lacking in 'omics approaches. The successful integration of 'omics, imaging and *in silico* methods can facilitate significant advances in understanding of the core functional principles at microbiome interfaces (Fig. 2). Here, we will briefly describe the cutting-edge methods, discuss their benefits, limitations, and complementarity within the context of the central principles of microbial interfaces.

Multi-omics

The core molecular biology toolbox for studying whole microbial communities comprises metagenomics, metatranscriptomics, metaproteomics, and metabolomics, targeting DNA, RNA, proteins, and metabolites, respectively (Box 1). Over the past decade, these approaches have all been used in isolation to drive unprecedented progress in microbial ecology. In the same way that these "meta-" methods facilitated a shift from organism-focused to community-based microbial ecology, their integration (known as "multi-omics", Box 1) converts the separate compositional, functional, and phenotypic approaches into a systems biology approach, capable of moving the field beyond taxonomic description into functional prediction. In a multi-omics approach, the core 'omics methods complement one another, either adding an additional modality or ameliorating the shortcomings of another.

Metagenomic data acts as a cornerstone, providing the blueprint of genetic potential against which metatranscriptomics and metaproteomics data can be aligned and the theoretical suite of pathways against which metabolomics data be mapped for the development of metabolic models (Box 1). Sample-specific metagenomic databases can reduce reliance on reference databases for other 'omics data types. They ensure functions are assigned to taxonomic units present in the sample as opposed to the nearest previously identified match, though a combination of both sample-specific and reference databases may be optimal (Jouffret et al. 2021). This is particularly important for environmental studies where the wealth of taxonomic diversity is poorly characterized, in contrast to mammalian-associated microbial communities such as humans and ruminants. For example, Rodríguez-Ramos et al. (2022) integrated metagenomics with their metaproteomic, metabolomic, and geochemical data, allowing them to resolve roles for specific bacteria, archaea, and viruses in carbon and nitrogen cycling in river sediments. Metagenomics-based approaches now benefit from cutting edge methods such

Box 1. Relevant -omics technologies

Multi-omics: generation and integrated data analysis, of two or more 'omics data types. Multi-omic approaches can provide cross-validation of component methods (e.g. proteins identified from metaproteomic data can be attributed to a host and genomic location via paired metagenomic data for the same sample) or generate novel insights (e.g. a highly expressed gene identified in metatranscriptomic data could map to multiple proteins indicating the occurrence of post-transcriptional splicing of the gene product).
Metagenomics: sequencing of all DNA in a sample with the aim of reconstructing the phylogenetic and metabolic diversity present in the original microbial community. Latest approaches include:

- Long read sequencing: produces higher contiguity in community reconstruction than short read technologies, resulting in metagenome-assembled genomes (MAGs) (Huang et al. 2023, Bickhart et al. 2022).
- High-throughput stable isotope probing (HT-SIP): provides insights into wild type microbial community metabolism by adding a labelled carbon source and detecting the accumulation of labelled carbon in the DNA backbone of organisms capable of consuming it (Nuccio et al. 2022).
- Metagenomic Hi-C: couples DNA cross-linking with metagenomic sequencing to cosequence DNA that is physically linked within host cells. This increases the number and quality of MAGs generated and can also link extrachromosomal elements such as plasmids to their hosts (Bickhart et al. 2019, 2022).

Metatranscriptomics: sequencing of all RNA in a sample to understand community level gene expression. Typically applied to reveal microbial community responses to biological, chemical, or physical changes in a given niche and particularly useful for studying the dynamics of temporal responses. Recent advances in metatranscriptomics include:

- Host–microbiome cosequencing: for host-associated microbiomes such as those found in the rhizosphere, human gut, or rumen, sequencing both host and microbial RNA can reveal networks of molecular communication between them (Law et al. 2022).
- Spatial metatranscriptomics: novel approaches such as seqFISH (see below) allow the projection of metatranscriptomic data into physical space, revealing important spatial aspects of transcription within or between microbes, and between microbes and their host tissues or physical niches (Saarenpää et al. 2023).

Metaproteomics: analysis of the complete suite of proteins from the variety of microorganisms present. This approach allows for a direct connection between the metagenome and the metabolic outputs (phenotype) of the microbes. By employing metaproteomics, insights into the functional aspects of microbiomes and investigate how they interact with their host environment can be gained. Additionally, this method enables the detection of post-translational modifications. Metaproteomic analysis can be approached through targeted or untargeted strategies (Sasson et al. 2022).
Metabolomics: The measurement of small molecules (chemicals with molecular masses of < 2000 Da e.g. polar metabolites, nonpolar, and lipids). Metabolomics can be targeted and untargeted, and the main platforms are MS (e.g. LC-MS and GC-MS) and NMR-based (Bauermeister et al. 2022). However, the coverage of metabolites is limited by the extent to which molecules can be extracted, detected, and identified. No single approach can capture all metabolites, however, different methods usually provide complementary data (Vernocchi et al. 2016, Gupta et al. 2022).

as long-read sequencing and Hi-C metagenomics, which generate greater assembly contiguity and numbers of metagenome-assembled genomes (Bickhart et al. 2019, Haryono et al. 2022). This allows higher resolution of the microbial community via access to intraspecies diversity, identification of new species and biosynthetic gene clusters. Such approaches can also reveal the relationships between taxa across kingdoms and linking of mobile genetic elements, which are critical agents in microbial community formation, function, adaptive fitness, and antimicrobial resistance transmission, to their hosts and environments (Bickhart et al. 2022, Hwang et al. 2023, Sereika et al. 2023). Finally, high-throughput sequencing with stable isotope probing (HT-SIP) is perhaps the most revolutionary metagenomic approach in that it allows genuine functional inference from metagenomic data by identifying the accumulation of isotopically labelled substrates in the DNA of specific species within an *in situ* microbial community (Nuccio et al. 2022).

In turn, metatranscriptomics augments metagenomic data with functional insights, revealing gene expression networks within complex communities and allowing functional assignments to taxonomic units (Box 1). For example, Van Goethem et al. (2021) effectively combined long-read metagenome assemblies and metatranscriptomics, exploiting the benefits of both, to reveal a network of dynamic responses of cyanobacterial biosynthetic gene cluster expression to light and wetting events. The latest approaches in metatranscriptomics, for microbial communities at host interfaces, involve cocapture of host and microbial community transcriptomes. Simultaneous gene expression analysis of the host and its associated microbiome can expose the complex molecular dialogue that coordinates their interactions. This can reveal synergistic effects arising in host–community interactions (Sola-Leyva et al. 2021) including mutualistic symbioses, such as mycorrhizal associations (Law et al. 2022), or organ–pathogen interactions during disease progression (Rajagopala et al. 2021). Future spatially resolved metatranscriptomic analyses of microbial communities at interfaces will increasingly require the precise delineation of spatial boundaries and time-dependent phase transitions. Alhough methods addressing are still in their infancy, such methods have been used to identify spatial bacterial burden in lung cancer cells (Wong-Rolle et al. 2022) and have yielded simultaneous host-transcriptome and microbiome wide characterization of Arabidopsis leaf tissues at 55 µm resolution (Saarenpää et al. 2023). These approaches in 'omics-based imaging, discussed below, remain challenging but will be essential to functionally profile complex microbiomes at spatial scales that are relevant for microbes and their host and that also reflect the high degree of spatial heterology of host and environmental interfaces.

Metaproteomics and metabolomics bridge the gap between genotype and phenotype connecting genes and their expression levels to proteins and metabolites (Box 1). Such data can then be interpreted in the context of the milieu of interactions in microbial communities and host and environmental interfaces (Gloag et al. 2013, Regmi et al. 2022). For example, Sasson et al. (2022) demonstrated the increased depth of insight possible

with metaproteomic data paired with metagenomic data in the rumen microbiome. Their study revealed associations between protein production profiles of specific metagenome-assembled genomes (in addition to phyla) and cattle feed efficiency phenotypes. Metaproteomics has a high degree of complementarity with metatranscriptomics and metabolomics. For example, a certain transcript, protein, or metabolite not identified via a single method might be identified via the other methods. Alternatively, such discordance between transcripts, proteins, and metabolites might result from a genuine biological process such as post-translational modifications to proteins or temporal and spatial dynamics of expression and function. Hagen et al. (2021) illustrated the complementarity of metatranscriptomic and metaproteomic methods as they elucidated the role of poorly characterized anaerobic fungi in plant fibre degradation via CAZyme production in the rumen.

Metabolomics enables characterization of metabolic functions and interactions occurring at host- and environment–microbiome interfaces (Box 1). Capturing both microbial and host endogenous metabolites and exogenous molecules enables system-wide interrogation of complex metabolic processes and relationships. These include production and exchange of nutrients, metabolic competitive, detoxification, or bioremediation processes as well as small molecule chemical signalling. Previous reviews provide comprehensive detail and examples of metabolomics use in plant, rumen, and human gut microbiome research (Vernocchi et al. 2016, Newbold and Ramos-Morales 2020, Gupta et al. 2022). Additionally, spatially resolved methods (e.g. mass spectrometry imaging (MSI)—see Box 2), fluxomics (using stable isotope labelling and mass spectrometry to quantify rates of metabolite flow through pathways in organisms or communities). The combination of both can provide further advances for improving our understanding and ability to manipulate metabolism and composition of total or functional-specific microbiomes at interfaces.

Advanced imaging techniques to study microbial communities

Whilst "omics"-based research can link compositional and functional dimensions of microbial community ecology on temporal scales, spatial dimensions remain a challenging frontier in the quest for a three-dimensional view of these unseen worlds (Fig. 2). Adding the spatial dimension is not only useful for studying specific interfaces and scaling up the knowledge from microscale to larger system level responses and functioning, but also enriches the pool of data available to modelling approaches. Imaging techniques have been successfully integrated with microbial community DNA, rRNA, mRNA, and metabolites revealing spatial aspects through both taxonomic and functional lenses (Shi et al. 2021). Such studies can help to refine inferences about interacting species, where colocalizing species are more likely to interact through metabolic and genetic exchange than spatially separated species. The methodological specifics of spatial "omics" are capably reviewed elsewhere, so here we aim to briefly highlight the most cutting-edge methods, examples of their application to microbial interfaces, and future possibilities. Taxonomically, HiPR-FISH (Box 2) has been demonstrated to spatially resolve microbes at the genus level in mouse gut and human oral microbiomes, however, it can be hampered by taxa-specific differences in ribosome accessibility, density, and competition between probes for the same ribosomal target (Shi et al. 2020). The seqFISH technique (Box 2), which targets mRNA transcripts, has been applied to reveal intercellular heterogeneity of gene expression for 105 target genes in communities of *P. aeruginosa* (Dar et al. 2021). Although application to a complex community is yet to be demonstrated, one can imagine the unprecedented level of information relevant to the central principles of microbial community assembly and function achievable, via biome-scale taxonomically and spatially resolved metatranscriptomics, if HiPR-FISH and seqFISH could be simultaneously implemented. As for the truly functional side of spatial "omics", MSI (Box 2) allows untargeted mapping of metabolites, proteins and lipids to infer the organization of metabolic function in a given sample. metaFISH pairs MSI and FISH to link microbial taxa and their metabolic functions in the same tissues sample. For example, metaFISH applied to deep sea mussels helped to identify linkages between the host metabolome and intracellular bacteria (Geier et al. 2020, Box 2). Other MSI methods include nanoSIMS and Raman microspectroscopy (Box 2). It is notable that most spatial "omics" techniques favour host-associated microbiomes, which generally have relatively lower diversity microbiomes on surfaces hence facilitate physical sectioning along a gradient or within the confines of a eukaryotic cell as opposed to the hyperdimensional, and higher diversity environmental microcosms such as soil. Techniques that address this will be critical in translating gains from host-associated research to environmental studies.

Just as each "omics" method has its strengths, each has their own technical and conceptual limitations. Biases, many of which are effectively unavoidable but can be minimized, may be introduced at all stages including sampling, extraction, sample preparation, sequencing, mass spectrometry, and via *in silico* methods (Nearing et al. 2021). Notable limitations include the relative, nonabsolute nature of abundance data for any molecule, the inability to disentangle microbial contributions from host in shared metabolic pathways and the fact that snapshot sampling cannot provide access to dynamic processes occurring over timescales shorter than practicable sampling intervals. Additionally, there are currently challenges in separating host and microbiome molecules prior to sequencing or delineating them *in silico* as well as incomplete reference databases for annotation of analytes or species identification. Overall, it is important to remember that 'omics studies may not always provide a full explanation for certain phenomena, but rather are hypothesis generating engines for subsequent follow up and validation.

Data integration and modelling of microbial dynamics

Multi-omics data should contain information regarding a myriad of intimately linked molecular phenomena, however, it is inherently large, highly dimensional, noisy, and sparse, which may render elucidating such linkages, their dynamics and driving factors a significant analytical challenge, particularly when 'omics layers chosen for a given experiment are discontinuous (e.g. metagenomics paired with metabolomics). Sequence-based methods are most readily integrated due to their direct relationship allowing dynamic insights between conditions via correlation between gene presence, gene expression, and protein expression. Correlation based approaches may also integrate nonsequence data types including metabolomic data and abiotic factors. This type of integration was demonstrated in a study of oleaginous microbial communities from a wastewater treatment plant, which revealed host-specific gene expression changes that are influenced by substrate availability and physiochemical parameters in anaerobic bioreactors (Herold et al. 2020). A variety of dimension reduction methods, which aim to identify biotic or abiotic factors

Box 2. Imaging

Fluorescence in situ hybridization (FISH): used for linking spatial information with phylogenetic and/or functional information, whereby fluorescent probes are designed to hybridize with conserved phylotyping genes or transcripts of interest (such as 16S rRNA genes or transcripts) allowing taxa to be visualized via fluorescence under confocal microscopy. Notable variants include:

- HiPR-FISH: high-phylogenetic resolution FISH utilizes binary encoding of fluorophore probes to significantly increase the number of probes that can be used, and hence the phylogenetic diversity that can be detected (Shi et al. 2020).
- seqFISH: application of FISH to mRNA molecules to reveal spatial dimensions of gene expression (Dar et al. 2021).
- metaFISH: multimodal method combining atmospheric pressure matrix-assisted laser desorption/ionization (AP-MALDI) with rRNA FISH to allow simultaneous resolution of taxa and metabolic landscape in tissue samples (Geier et al. 2020).

Mass spectrometry imaging (MSI): a technique for resolving chemical and metabolic landscapes in fixed tissue samples. Samples are typically ablated and ionized to infer the localized molecular composition. A prominent example is *nanoSIM S*(nanoscale secondary ion mass spectrometry), which involves integration of stable isotopes into substrates that are then introduced to a bacterial community (Chadwick et al. 2019). MSI of finely sectioned tissue samples then allows inference of metabolism of these substrates at single cell resolution.

Raman microspectroscopy: a nondestructive alternative to MSI approaches, relying on detection of changes in the frequency of light applied to a sample and allowing downstream 'omics analyses on the same sample (Ivleva et al. 2017).

that explain variation in "omics data" or act as indicators for a given treatment or sample, are increasingly popular as correlative approaches encounter an unmanageable number of comparisons in multi-omics datasets. Packages enabling these methods include mixOmics, MOFA, and MEFISTO, the latter of which handles spatio-temporal data that fails assumptions of the former models (Rohart et al. 2017, Argelaguet et al. 2020, Velten et al. 2022). These approaches can also handle discontiguous combinations of "omics" data. Beyond these modes of integration, modelling approaches driven by multi-omics data, modern computing power, and statistical methods take data integration from the descriptive and explanatory into the area of simulation, prediction, hypothesis generation and testing.

Computational modelling can complement and expand experimental techniques in exploring the drivers of assembly, composition, and function of interface microbiome communities. Mathematical models can provide a framework to facilitate the integration and interpretation of experimental data, including multi-omics (Dahal et al. 2020), to gain a system-wide perspective of microbiome function. Their generality means they can be applied to any interface-microbiome system and model predictions can be used to generate hypotheses. For example, modelling can help make predictions about how host and microbiome responds to perturbation, cross-species interactions, spatiotemporal dynamics, and emergent community properties, that can then be experimentally tested. Microbiome modelling approaches can be data-driven, or process based, encompassing a broad spectrum that spans from ecological scales to molecular and metabolic levels (refer to reviews by Qian et al. 2021, Nagarajan et al. 2022, van den Berg et al. 2022), as well as physics-based.

As an example of a data-driven approach, ecological models can predict and analyse population dynamics, including temporal changes in abundances. This makes them useful for examining microbial and community assembly, growth, and succession. Although ecological models offer a comprehensive understanding of microbe–microbe interactions at a macroscopic level, they often lack insights into the underlying molecular mechanisms. However, when combined with other modelling approaches, they can synergistically reveal mechanistic foundations. For example, Clark et al. (2021) used a combination of ecological and regression modelling to design a beneficial high butyrate-producing community from human-gut associated microbes. A dynamic ecological model (generalized Lotka–Volterra) was used to accurately predict community assembly and paired with a linear regression model to establish a connection between community composition and metabolic function. Through this comprehensive approach, Clark et al. (2021) identified hydrogen sulphide production, environmental pH, and resource competition as critical factors influencing butyrate production.

Genome-scale metabolic modelling, a process-based approach, employs mathematical representations of metabolic reactions encoded in an organism or community's (meta)genome. Genome-scale metabolic models (GEMs) enable the simulation of metabolic phenotypes under specific constraints (e.g. through flux-balance analysis, FBA; Price et al. 2004). Growth rates, intracellular fluxes, secretion or uptake rates, and responses to interventions or perturbations can be predicted using FBA and GEMs (Heinken et al. 2021). Application of GEMs to interfacial microbial communities, could enable the exploration of nutrient–microbe, microbe–microbe and host–microbe metabolic interactions, thus revealing mechanistic insights into community assembly rules and host responses (Colarusso et al. 2021). Furthermore, GEMs can be used as input for dynamic agent-based models to predict microbiome metabolism and growth through space and time to better understand how nutrient accessibility and diffusion or convection of mass affect community dynamics in a spatially structured environment. Indeed, tools such as CASINO (Shoaie et al. 2015), BacArena (Bauer et al. 2017), COMETS (Harcombe et al. 2014), and IndiMeSH (Borer et al. 2022) have been developed to facilitate this. For example, Borer et al. (2022) used spatiotemporal (IndiMeSH) community GEMs, representing communities in soil environments, to predict how the emergent bacterial community composition is shaped by trophic interactions and diffusion constraints (in the context of soil pore spaces). The model findings were validated *in vitro* by synthetic communities. Their results could be applied to inform manipulations in soil communities for example, to improve carbon sequestration and nutrient cycling. This highlights the benefits of harnessing genomics, modelling, spatial representations, and synthetic communities to enhance prediction of microbiome function in specific interface niches.

While promising, it should be noted that current GEM approaches have mostly been limited to a small number of species (i.e. up to five species). The challenge of scaling them needs to be addressed for them to have utility for complex multispecies microbiomes. Databases of GEMs have been developed to facilitate construction of compartmentalized multispecies GEMs, including host–microbiome models. For example, AGORA and AGORA2 (Heinken et al. 2023) contain GEMs of human gut microbiota

members (1738 species and 7302 strains), which are compatible with Recon2 (human GEM; Thiele et al. 2013), while modelSEED (Seaver et al. 2021) and plantSEED (Seaver et al. 2018) databases contain plant, bacteria, and fungal GEMs in plant–root–soil communities as well as a biochemical database to facilitate new model reconstructions. Furthermore, improvements in genome annotation and the incorporation of functional omics and phenotype data will aid in improving the accuracy of GEMs and thereby their utility in the emerging microbiome community FBA space.

Finally, physics-based mechanistic models (PBMM) can incorporate physical principles into microbiome community modelling and offer an approach to explore the interplay between physical and biochemical processes, and microbial dynamics. PBMM involves the development of mathematical formulas that capture the essential laws of physics and biochemical principles (Baker et al. 2018, Kalirad and Sommer 2022). These formulas aim to accurately predict the expected inputs and outputs of the model, aligning them with real-life observations. Physical factors, including fluid flow (e.g. water movement in soil), diffusion and nutrient transport, pH gradients, physical barriers (e.g. gut mucus layers), and structure (e.g. plant root architecture) can be modelled along with biological and biochemical processes (e.g. microbial recruitment, attachment, growth and succession, genetic regulation, host–microbe, and microbe–microbe interactions). Combining these parameters enables simulation of microbial and community behaviours within specific environments (e.g. bacterial colonization of root tips in soil, and food digestion in the rumen or human gut). For example, Dupuy and Silk (2016) developed a mechanistic model of the root–soil compartment to analyse the factors that explain the maintenance of microorganisms on the tip of growing root. Further, Labavić et al. (2022) demonstrated the application of hydrodynamic laws, bacterial growth kinetics, and metabolic activity to highlight that specific genetic variants exhibited a greater likelihood of achieving dominance and persistence in the human gut environment in contrast with a well-mixed chemostat system. This implies caution in the interpretation of in vitro studies of the gut. While PBMMs show promise in making predictions about real-world microbiome scenarios, the complexity and uncertainty of the system can be a limitation. PBMMs require empirical data for model development, parameter estimation, and validation. Therefore, PBMMs are commonly designed for a specific aim and consider only limited and relevant aspects of the system they aim to model.

While *in silico* modelling approaches offer advantages for exploring complex interface microbiome communities, significant challenges remain. These include the inherent biological and physical complexity of these interface systems and the computational resources required for extensive mathematical formulations. Improving high-throughput generation and integration of phenotype, multi-omics data, spatial and temporal data, enhancing parameterization and validation, promoting standardization, and advancing computational infrastructure will help advance *in silico* modelling in microbiome research. This will ultimately lead to a deeper understanding of interface microbiome dynamics and their implications for diverse fields such as agriculture, and ecosystem, animal, and human health.

Importance for One Health interventions

Here, we have highlighted the complex relationship between microorganisms and their respective hosts (or environment), the parallels and differences across different host and environmental interfaces, as well as their significant effects in relation to One Health. Research into the links among microbiomes of soil, plants, animals, and humans has underscored the possibility of interactions across systems that extend beyond direct transfer of microbes. For instance, when the soil microbiome is effectively managed, it not only bolsters plant health but also improves the nutritional value of the crops through improved nutrient availability (Babin et al. 2021). In turn, consumption of these plants can influence the composition and function of animal and human gut microbiomes, producing a One Health nexus between soil and GI microbiomes. This connectivity can also be leveraged when designing deliberate interventions to optimize microbiome function.

Functional prediction has emerged as a crucial tool in understanding and harnessing the potential of microbiomes. Additionally, as functional potential and microbial taxonomic composition are not necessarily linearly related due to functional redundancy, effective functional prediction is necessary to determine and manage the contribution of microbial communities to ecosystem processes. We have discussed the cutting-edge technologies, including omics and imaging-based approaches, to decipher the metabolic potential, rules governing assembly, and intricate interactions within microbial communities. By integrating these data through advanced bioinformatics and *in silico* modelling approaches, the ability to predict the functional capabilities of microbiomes has vastly improved. Further technological and informatics development, including better spatial and temporal resolution and pipelines to support the integration of experimental and mathematical modelling methods, will drive future advances in our ability to predict and manipulate microbiome function.

Current deliberate intervention strategies have proven effective in leveraging the microbiome's potential to promote host health and environmental sustainability. For example, microbial inoculants have been promoted with agricultural crops to enhance nutrient uptake, improve plant resilience to stress, and reduce reliance on chemical inputs (Backer et al. 2018). The reduced reliance on chemicals has One Health implications as well, with lower risk of biomagnification of those chemicals as well as overall improved system health. Similarly, in human health, deliberate manipulation of the gut microbiome through probiotics, prebiotics, and faecal microbiota transplantation has shown promise in managing various disorders and improving overall well-being. However, with many of these strategies, the mechanisms are still not fully understood. For example, though faecal microbiota transplants can be highly effective at treating *C. difficile* infection post antibiotic stress (Baunwall et al. 2022), these communities are undefined with unknown interactions that currently require careful customization due to unpredictable nature of outcomes (Kazemian et al. 2020). The unknown contributions of individual constituents in these complex communities make it challenging to optimize or tailor microbial treatments to target specific functional outcomes.

Despite these current challenges, the area of synthetic community design has growing potential to enable precision microbiome manipulation. Synthetic microbiomes, with reduced complexity and control of initial community composition, have provided insights into causal interactions influencing community assembly and functional outcomes (Venturelli et al. 2018, de Souza et al. 2020). Moreover, successful applications of synthetic communities have been demonstrated in experimental models. For example, Niu et al. (2017) introduced a simplified synthetic community to axenic maize roots, which successfully suppressed the growth of the plant-pathogenic fungus *Fusarium verticillioides*, thereby conferring protection to the host plant. However, there are still challenges with the widespread industrial application of synthetic microbiomes, particularly in more complex interface systems. This

is primarily because of our incomplete understanding of the inherent associated risks (e.g. spread of antimicrobial resistance genes) and fundamental processes that govern microbiome assembly, such as recruitment, attachment, growth and succession, and trophic interactions (Fig. 1). Thorough understanding of these elements is necessary to accurately predict how a novel synthetic community would establish, function within, and alter a complex environment that may already be populated by a diverse array of species.

Microbiome engineering approaches are also emerging as a viable option to design probiotics or inoculants for specific environmental, agricultural, or human health benefits. This process entails introducing functional modifications to one or more organisms within a community, thereby influencing the overall performance of the entire microbiome. Approaches can involve *ex situ* engineering of organisms prior to community reintegration to assess functional changes, or *in situ* modification of multiple organisms or communities. Althouh the latter is the most challenging, it is potentially the most rewarding as it works with the native community and does not require reintroduction of modified species, which may not be competitive (reviewed by Ke et al. 2021). Briefly, techniques to enable high-throughput functional screening, a necessity to assess the effects of any targeted intervention, include transposon mutagenesis (TnSeq) and CRISPR-enabled trackable genome engineering (CREATE). Targeted methods for integration of synthetic genetic material include conjugative broad host range (BHR) plasmids, integrative and conjugative elements (ICE), chassis-independent recombinase-assisted genome engineering (CRAGE), environmental transformation sequencing and DNA-editing all-in-one RNA-guided CRISPR–Cas transposase (ET-Seq + DART; Rubin et al. 2022), and MAGIC (metabolomics alteration of gut microbiome in situ conjugation). Applied examples include functionalized soil amendments (Pham et al. 2017, Mathes et al. 2020), transfer of IncP plasmids from diverse hosts to multiple bacterial phyla in a soil community (Klümper et al. 2015), mini-ICE-mediated delivery of a biosynthetic gene cluster to a synthetic soil community *in situ* and genomic modification in 297 microbial species within the murine gut (Brophy et al. 2018, Ronda et al. 2019). Due to their novelty and practical limitations associated with the complexity of the methods, widespread application of these techniques to the key microbial interfaces under review is still limited. Nonetheless, the scale of benefit achievable by their successful implementation will continue to drive research and innovation in this space.

Microbiome interventions should consider the multilayered interactions and connectivity between hosts or environments and microbiome niches, which drive community behaviour and phenotypes. This complexity provides challenges and opportunities to engineer or influence microbiomes. Advancements in functional prediction and deliberate interventions have paved the way for precision microbiome manipulation, enabling researchers to optimize microbial communities for improved host and environmental well-being. By further exploring the complexities of microbiome assembly, understanding the ecological and molecular mechanisms that shape these communities, and leveraging technological advancements, we can unlock the full potential of microbiomes to achieve beneficial outcomes for One Health.

Conclusions

The Anthropocene is a phase in our planet's history marked by the impact of human activities on planetary health, largely due to unprecedented levels of human population growth, rapid industrialization, and the relentless exploitation of natural resources. Already, shrinking habitats, biodiversity loss, and the extinction of keystone species have begun to undermine the resilience of fragile ecosystems worldwide. Meanwhile, the escalating frequency and intensity of extreme weather events driven by climate change is placing increasing strain on existing agricultural systems and supply chains to maintain global food security and ecosystem health. Finally, the steady rise of AMR genes in clinical and agricultural settings are growing existential threats, as the list of effective treatment options that are critical to modern medicine continues to shrink. Despite the seemingly insurmountable nature of these challenges, the Anthropocene has also seen the emergence of new technologies that have ushered in a greater understanding of the natural world and an increased appreciation for the interconnectedness of human, animal, plant, and ecosystem health. This One Health framework encourages integrative approaches, with the collaborative efforts of diverse scientific disciplines shaping new global health policies, conservation strategies, and the implementation of sustainable and evidence-based solutions. No field of scientific endeavour is better placed to contribute to this framework than that of microbiome research, which over the past decade alone, has provided viable alternatives to antibiotics in the treatment of human diseases, microbial inoculants to boost plant productivity and resilience, and soil amendments to enhance carbon sequestration. What the next decade of microbiome research holds for the realization of One Health aims makes for exciting speculation. Will we see the commonplace prescription of precision-formulated microbial communities to treat patients with GI issues? Will it be possible to completely replace synthetic fertilizers and chemical pesticides across agriculture with microbial inocula and still meet global food requirements? Will the restoration of forests and grasslands worldwide involve seeding these ecosystems with bespoke microbial communities to ensure plant vigour and the efficient accumulation of stable soil organic carbon? The body of literature covered in this review illustrates a growing understanding of the core principles governing microbiome assembly across interfaces crucial to One Health and highlights the technologies that will be needed to achieve these goals and promote the well-being of all life within our rapidly changing environment and world.

Acknowledgements

The preparation of this manuscript was supported through funding from CSIRO Microbiomes for One Systems Health (MOSH)-Future Science Platform. It was also supported by the Business Units, Agriculture & Food; Health & Biosecurity; Environment and Data61, CSIRO Australia.

Conflict of interest: None declared.

References

Aagaard K, Ma J, Antony KM *et al.* The placenta harbors a unique microbiome HHS public access author manuscript. *Sci Transl Med* 2014;**6**:237–65.

Abdelaal K, Alkahtani M, Attia K *et al.* The role of plant growth-promoting bacteria in alleviating the adverse effects of drought on plants. *Biology* 2021;**10**:520. https://doi.org/10.3390/biology10060520.

Abdelfattah A, Wisniewski M, Schena L *et al.* Experimental evidence of microbial inheritance in plants and transmission routes

from seed to phyllosphere and root. *Environ Microbiol* 2021;**23**: 2199–214.

Adeleke B, Fadiji A, Ayilara M *et al.* Strategies to enhance the use of endophytes as bioinoculants in agriculture. *Horticulturae* 2022;**8**:498.

Ahearn-Ford S, Berrington JE, Stewart CJ. Development of the gut microbiome in early life. *Exp Physiol* 2022;**107**:415–21.

Aho VTE, Houser MC, Pereira PAB *et al.* Relationships of gut microbiota, short-chain fatty acids, inflammation, and the gut barrier in Parkinson's disease. *Mol Neurodegen* 2021;**16**. https://doi.org/10.1186/s13024-021-00427-6.

Ajilogba CF, Olanrewaju OS, Babalola OO. Plant growth stage drives the temporal and spatial dynamics of the bacterial microbiome in the rhizosphere of *Vigna subterranea*. *Front Microbiol* 2022;**13**. https://doi.org/10.3389/fmicb.2022.825377.

Alcaraz LD, Moreno-Hagelsieb G, Eguiarte LE *et al.* Understanding the evolutionary relationships and major traits of *Bacillus* through comparative genomics. *BMC Genomics* 2010;**11**:332.

Aleklett K, Rosa D, Pickles BJ *et al.* Community assembly and stability in the root microbiota during early plant development. *Front Microbiol* 2022;**13**. https://doi.org/10.3389/fmicb.2022.826521.

Álvarez-Garrido L, Viñegla B, Hortal S *et al.* Distributional shifts in ectomycorrizhal fungal communities lag behind climate-driven tree upward migration in a conifer forest-high elevation shrubland ecotone. *Soil Biol Biochem* 2019;**137**:107545. https://doi.org/10.1016/j.soilbio.2019.107545.

Amat S, Holman DB, Schmidt K *et al.* Characterization of the microbiota associated with 12-week-old bovine fetuses exposed to divergent in utero nutrition. *Front Microbiol* 2022;**12**. https://doi.org/10.3389/fmicb.2021.771832.

Anderson AC, Rothballer M, Altenburger MJ *et al.* Long-term fluctuation of oral biofilm microbiota following different dietary phases. *Appl Environ Microb* 2020;**86**. https://doi.org/10.1128/AEM.01421-20.

Antunes LCM, Han J, Ferreira RBR *et al.* Effect of antibiotic treatment on the intestinal metabolome. *Antimicrob Agents Chemother* 2011;**55**:1494.

Argelaguet R, Arnol D, Bredikhin D *et al.* MOFA+: a statistical framework for comprehensive integration of multi-modal single-cell data. *Genome Biol* 2020;**21**:111.

Arias SL, Brito IL. Biophysical determinants of biofilm formation in the gut. *Curr Opin Biomed Eng* 2021;**18**:100275.

Attwood GT, Wakelin SA, Leahy SC *et al.* Applications of the soil, plant and rumen microbiomes in pastoral agriculture. *Front Nutr* 2019;**6**:107.

Australian Institute of Health and Welfare. *National Core Maternity Indicators*. Canberra, 2023.

Awany D, Allali I, Dalvie S *et al.* Host and microbiome genome-wide association studies: current state and challenges. *Front Genet* 2019;**9**. https://doi.org/10.3389/fgene.2018.00637.

Babin D, Leoni C, Neal AL *et al.* Editorial to the thematic topic "Towards a more sustainable agriculture through managing soil microbiomes". *FEMS Microbiol Ecol* 2021;**97**. https://doi.org/10.1093/femsec/fiab094.

Bach A, Calsamiglia S, Stern MD. Nitrogen metabolism in the rumen. *J Dairy Sci* 2005;**88**:E9–E21.

Backer R, Rokem JS, Ilangumaran G *et al.* Plant growth-promoting rhizobacteria: context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. *Front Plant Sci* 2018;**9**. https://doi.org/10.3389/fpls.2018.01473.

Bäckhed F, Roswall J, Peng Y *et al.* Dynamics and stabilization of the human gut microbiome during the first year of life. *Cell Host Microbe* 2015;**17**:690–703.

Baker RE, Peña JM, Jayamohan J *et al.* Mechanistic models versus machine learning, a fight worth fighting for the biological community?. *Biol Lett* 2018;**14**:20170660, https://doi.org/10.1098/RSBL.2017.0660.

Baliyan N, Dhiman S, Dheeman S *et al.* Bacteriophage cocktails as antibacterial agents in crop protection. *Environ Sustain* 2022;**5**:305–11.

Banasiak J, Borghi L, Stec N *et al.* The full-size ABCG transporter of *Medicago truncatula* is involved in strigolactone secretion, affecting arbuscular mycorrhiza. *Front Plant Sci* 2020;**11**:491370.

Banerjee S, van der Heijden MGA. Soil microbiomes and one health. *Nat Rev Micro* 2023;**21**:6–20.

Barrett E, Ross RP, O'Toole PW *et al.* γ-Aminobutyric acid production by culturable bacteria from the human intestine. *J Appl Microbiol* 2012;**113**:411–7.

Bauer E, Zimmermann J, Baldini F *et al.* BacArena: individual-based metabolic modeling of heterogeneous microbes in complex communities. *PLoS Comput Biol* 2017;**13**:e1005544.

Bauermeister A, Mannochio-Russo H, Costa-Lotufo LV *et al.* Mass spectrometry-based metabolomics in microbiome investigations. *Nat Rev Micro* 2022;**20**:143–60.

Baunwall S, Andreasen S, Hansen M *et al.* Faecal microbiota transplantation for first or second *Clostridioides difficile* infection (EarlyFMT): a randomised, double-blind, placebo-controlled trial. *Lancet Gastroenterol Hepatol* 2022;**7**:1083–91.

Bergman EN. Energy contributions of volatile fatty acids from the gastrointestinal tract in various species. *Physiol Rev* 1990;**70**: 567–90.

Berne C, Ducret A, Hardy GG *et al.* Adhesins involved in attachment to abiotic surfaces by Gram-negative bacteria. *Microbiol Spectr* 2015;**3**:26350310.

Beveridge TJ, Makin SA, Kadurugamuwa JL *et al.* Interactions between biofilms and the environment. *FEMS Microbiol Rev* 1997;**20**: 291–303.

Bhattacharyya SS, Ros GH, Furtak K *et al.* Soil carbon sequestration—an interplay between soil microbial community and soil organic matter dynamics. *Sci Total Environ* 2022;**815**:152928.

Bi Y, Cox MS, Zhang F *et al.* Feeding modes shape the acquisition and structure of the initial gut microbiota in newborn lambs. *Environ Microbiol* 2019;**21**:2333–46.

Bickhart DM, Kolmogorov M, Tseng E *et al.* Generating lineage-resolved, complete metagenome-assembled genomes from complex microbial communities. *Nat Biotechnol* 2022;**40**: 711–9.

Bickhart DM, Watson M, Koren S *et al.* Assignment of virus and antimicrobial resistance genes to microbial hosts in a complex microbial community by combined long-read assembly and proximity ligation. *Genome Biol* 2019;**20**:153.

Böhme A, Risse-Buhl U, Küsel K. Protists with different feeding modes change biofilm morphology. *FEMS Microbiol Ecol* 2009;**69**:158–69.

Boillat M, Hammoudi PM, Dogga SK *et al.* Neuroinflammation-associated aspecific manipulation of mouse predator fear by *Toxoplasma gondii*. *Cell Rep* 2020;**30**:320–334.e6.

Borer B, Kleyer H, Or D. Primary carbon sources and self-induced metabolic landscapes shape community structure in soil bacterial hotspots. *Soil Biol Biochem* 2022;**168**:108620.

Boro M, Sannyasi S, Chettri D *et al.* Microorganisms in biological control strategies to manage microbial plant pathogens: a review. *Arch Microbiol* 2022;**204**:666.

Bowman JGP, Firkins JL. Effects of forage species and particle size on bacterial cellulolytic activity and colonization in situ. *J Anim Sci* 1993;**71**:1623–33.

Braegger C, Chmielewska A, Decsi T *et al.* Supplementation of infant formula with probiotics and/or prebiotics: a systematic review and comment by the ESPGHAN committee on nutrition. *J Pediatr Gastroenterol Nutr* 2011;**52**:238–50.

Brinkac L, Voorhies A, Gomez A *et al.* The threat of antimicrobial resistance on the human microbiome. *Microb Ecol* 2017;**74**:1001–8.

Brophy JAN, Triassi AJ, Adams BL *et al.* Engineered integrative and conjugative elements for efficient and inducible DNA transfer to undomesticated bacteria. *Nat Microbiol* 2018;**3**:1043–53.

Bruijning M, Henry LP, Forsberg SKG *et al.* Natural selection for imprecise vertical transmission in host-microbiota systems HHS Public Access. *Nat Ecol Evol* 2022;**6**:77–87.

Burmølle M, Hansen LH, Sørensen SJ. Establishment and early succession of a multispecies biofilm composed of soil bacteria. *Microb Ecol* 2007;**54**:352–62.

Butler A, Hur B, Junior M *et al.* Absorbing roots areas and transpiring leaf areas at the tropical forest and savanna boundary in Brazil. In: *Savannas: Climate, Biodiversity and Ecological Significance*. New York: Nova Science Publishers, 2013.

Calderón-amor J, Gallo C. Dairy calf welfare and factors associated with diarrhea and respiratory disease among chilean dairy farms. *Animals* 2020;**10**:1115.

Cardinale S, Kadarmideen HN. Host genome–metagenome analyses using combinatorial network methods reveal key metagenomic and host genetic features for methane emission and feed efficiency in cattle. *Front Genet* 2022;**13**:81.

Carniello V, Peterson BW, van der Mei HC *et al.* Physico-chemistry from initial bacterial adhesion to surface-programmed biofilm growth. *Adv Colloid Interface Sci* 2018;**261**:1–14.

Carrión VJ, Perez-Jaramillo J, Cordovez V *et al.* Pathogen-induced activation of disease-suppressive functions in the endophytic root microbiome. *Science* 2019;**366**:606–12.

Castrillo G, Teixeira PJPL, Paredes SH *et al.* Root microbiota drive direct integration of phosphate stress and immunity. *Nature* 2017;**543**:513–8.

Chabé M, Lokmer A, Ségurel L. Gut protozoa: friends or foes of the human gut microbiota?. *Trends Parasitol* 2017;**33**:925–34.

Chadwick GL, Jiménez Otero F, Gralnick JA *et al.* NanoSIMS imaging reveals metabolic stratification within current-producing biofilms. *Proc Natl Acad Sci USA* 2019;**116**:20716–24.

Chagnot C, Listrat A, Astruc T *et al.* Bacterial adhesion to animal tissues: protein determinants for recognition of extracellular matrix components. *Cell Microbiol* 2012;**14**:1687–96.

Chaluvadi S, Bennetzen JL. Species-associated differences in the below-ground microbiomes of wild and domesticated setaria. *Front Plant Sci* 2018;**9**. https://doi.org/10.3389/fpls.2018.01183.

Chaparro JM, Badri DV, Vivanco JM. Rhizosphere microbiome assemblage is affected by plant development. *ISME J* 2014;**8**:790–803.

Christopherson MR, Dawson JA, Stevenson DM *et al.* Unique aspects of fiber degradation by the ruminal ethanologen *Ruminococcus albus 7* revealed by physiological and transcriptomic analysis. *BMC Genomics* 2014;**15**:1066.

Chynoweth RJ, Rolston MP, Kelly M *et al.* Control of blind seed disease (*Gloeotinia temulenta*) in perennial ryegrass (*Lolium perenne*) seed crops and implications for endophyte transmission. *Agron New Zeal* 2012;**42**:32560813.

Clark RL, Connors BM, Stevenson DM *et al.* Design of synthetic human gut microbiome assembly and butyrate production. *Nat Commun* 2021;**12**. https://doi.org/10.1038/s41467-021-22938-y.

Colarusso AV, Goodchild-Michelman I, Rayle M *et al.* Computational modeling of metabolism in microbial communities on a genome-scale. *Curr Opin Syst Biol* 2021;**26**:46–57.

Compton KK, Scharf BE. Rhizobial chemoattractants, the taste and preferences of legume symbionts. *Front Plant Sci* 2021;**12**:686465.

Conlon M, Bird A. The impact of diet and lifestyle on gut microbiota and human health. *Nutrients* 2014;**7**:17–44.

Cox LM, Blaser MJ. Antibiotics in early life and obesity. *Nat Rev Endocrinol* 2015;**11**:182–90.

Croes CL, Moens S, van Bastelaere E *et al.* The polar flagellum mediates *Azospirillum brasilense* adsorption to wheat roots. *J Gen Microbiol* 1993;**139**:2261–9.

Cunningham HC, Austin KJ, Powell SR *et al.* Potential response of the rumen microbiome to mode of delivery from birth through weaning. *Transl Anim Sci* 2018;**2**:S35–8.

Dahal S, Yurkovich JT, Xu H *et al.* Synthesizing systems biology knowledge from Omics using genome-scale models. *Proteomics* 2020;**20**. https://doi.org/10.1002/pmic.201900282.

Dar D, Dar N, Cai L *et al.* Spatial transcriptomics of planktonic and sessile bacterial populations at single-cell resolution. *Science* 2021;**373**. https://doi.org/10.1126/science.abi4882.

Darcy JL, Washburne AD, Robeson MS *et al.* A phylogenetic model for the recruitment of species into microbial communities and application to studies of the human microbiome. *ISME J* 2020;**14**:1359–68.

Dash NR, Khoder G, Nada AM *et al.* Exploring the impact of *Helicobacter pylori* on gut microbiome composition. *PLoS ONE* 2019;**14**:e0218274.

De Mulder T, Goossens K, Peiren N *et al.* Exploring the methanogen and bacterial communities of rumen environments: solid adherent, fluid and epimural. *FEMS Microbiol Ecol* 2016;**93**:fiw251.

de Souza RSC, Armanhi JSL, Arruda P. From microbiome to traits: designing synthetic microbial communities for improved crop resiliency. *Front Plant Sci* 2020;**11**. https://doi.org/10.3389/fpls.2020.01179.

De Weirdt R, Van de Wiele T. Micromanagement in the gut: microenvironmental factors govern colon mucosal biofilm structure and functionality. *npj Biofilms Microbiomes* 2015;**1**:15026.

DeFlaun MF, Oppenheimer SR, Streger S *et al.* Alterations in adhesion, transport, and membrane characteristics in an adhesion-deficient pseudomonad. *Appl Environ Microb* 1999;**65**:759–65.

Derrien M, van Hylckama Vlieg JET. Fate, activity, and impact of ingested bacteria within the human gut microbiota. *Trends Microbiol* 2015;**23**:354–66.

Dill-McFarland KA, Weimer PJ, Breaker JD *et al.* Diet influences early microbiota development in dairy calves without long-term impacts on milk production. *Appl Environ Microb* 2019;**85**. https://doi.org/10.1128/AEM.02141-18.

Dimkpa C, Weinand T, Asch F. Plant-rhizobacteria interactions alleviate abiotic stress conditions. *Plant Cell Environ* 2009;**32**:1682–94.

Dixit S, Kumar S, Sharma R *et al.* Rumen multi-omics addressing diet–host–microbiome interplay in farm animals: a review. *Anim Biotechnol* 2023;**34**:3187–205. https://doi.org/10.1080/10495398.2022.2078979.

Dominguez-Bello MG, Godoy-Vitorino F, Knight R *et al.* Role of the microbiome in human development. *Gut* 2019;**68**:1108–14.

Donaldson GP, Lee SM, Mazmanian SK. Gut biogeography of the bacterial microbiota. *Nat Rev Micro* 2016;**14**:20–32.

Donn S, Kirkegaard JA, Perera G *et al.* Evolution of bacterial communities in the wheat crop rhizosphere. *Environ Microbiol* 2015;**17**:610–21.

Doron I, Kusakabe T, Iliev ID. Immunoglobulins at the interface of the gut mycobiota and anti-fungal immunity. *Semin Immunol* 2023;**67**:101757.

Dow L, Gallart M, Ramarajan M *et al.* Streptomyces and their specialised metabolites for phytopathogen control—comparative in vitro and in planta metabolic approaches. *Front Plant Sci* 2023;**14**. https://doi.org/10.3389/fpls.2023.1151912.

Du Y, Gao Y, Hu M *et al.* Colonization and development of the gut microbiome in calves. *J Anim Sci Biotechnol* 2023;**14**:1–15.

Dupuy LX, Silk WK. Mechanisms of early microbial establishment on growing root surfaces. *Vadose Zone J* 2016;**15**:1–13.

Durán P, Ellis TJ, Thiergart T *et al.* Climate drives rhizosphere microbiome variation and divergent selection between geographically distant *Arabidopsis* populations. *New Phytol* 2022;**236**:608–21.

Elolimy A, Alharthi A, Zeineldin M *et al.* Supply of methionine during late-pregnancy alters fecal microbiota and metabolome in neonatal dairy calves without changes in daily feed intake. *Front Microbiol* 2019;**10**. https://doi.org/10.3389/fmicb.2019.02159.

Enayathullah MG, Parekh Y, Banu S *et al.* Gramicidin S and melittin: potential anti-viral therapeutic peptides to treat SARS-CoV-2 infection. *Sci Rep* 2022;**12**. https://doi.org/10.1038/s41598-022-07341-x.

Etzold S, Kober OI, MacKenzie DA *et al.* Structural basis for adaptation of lactobacilli to gastrointestinal mucus. *Environ Microbiol* 2014;**16**:888–903.

Ezenwa VO, Gerardo NM, Inouye DW *et al.* Animal behavior and the microbiome. *Science* 2012;**338**:198–9.

Faust K, Sathirapongsasuti JF, Izard J *et al.* Microbial co-occurrence relationships in the human microbiome. *PLoS Comput Biol* 2012;**8**:e1002606.

Fierer N. Embracing the unknown: disentangling the complexities of the soil microbiome. *Nat Rev Micro* 2017;**15**:579–90.

Fierer N, Jackson RB. The diversity and biogeography of soil bacterial communities. *Proc Natl Acad Sci USA* 2006;**103**:626–31.

Flemming H-C, Wingender J, Szewzyk U *et al.* Biofilms: an emergent form of bacterial life. *Nat Rev Micro* 2016;**14**:563–75.

Flemming H-C, Wuertz S. Bacteria and archaea on Earth and their abundance in biofilms. *Nat Rev Micro* 2019;**17**:247–60.

Fragiadakis GK, Smits SA, Sonnenburg ED *et al.* Links between environment, diet, and the hunter-gatherer microbiome. *Gut Microbes* 2019;**10**:216–27.

Frank AC, Saldierna JP, Shay JE. Transmission of bacterial endophytes. *Microorg* 2017;**5**:70.

Freestone P, Lyte M. Stress and microbial endocrinology: prospects for ruminant nutrition. *Animal* 2010;**4**:1248–57.

Ganz HH, Turner WC, Brodie EL *et al.* Interactions between *Bacillus anthracis* and plants may promote anthrax transmission. *PLoS Negl Trop Dis* 2014;**8**:e2903-.

Gao Z, Karlsson I, Geisen S *et al.* Protists: puppet masters of the rhizosphere microbiome. *Trends Plant Sci* 2019;**24**:165–76.

Geier B, Sogin EM, Michellod D *et al.* Spatial metabolomics of in situ host–microbe interactions at the micrometre scale. *Nat Microbiol* 2020;**5**:498–510.

Ghiboub M, Verburgt CM, Sovran B *et al.* Nutritional therapy to modulate tryptophan metabolism and aryl hydrocarbon-receptor signaling activation in human diseases. *Nutrients* 2020;**12**:1–21.

Gilbert JA, Quinn RA, Debelius J *et al.* Microbiome-wide association studies link dynamic microbial consortia to disease. *Nature* 2016;**535**:94–103.

Gilbert RA, Townsend EM, Crew KS *et al.* Rumen virus populations: technological advances enhancing current understanding. *Front Microbiol* 2020;**11**. https://doi.org/10.3389/fmicb.2020.00450.

Gloag ES, Turnbull L, Huang A *et al.* Self-organization of bacterial biofilms is facilitated by extracellular DNA. *Proc Natl Acad Sci USA* 2013;**110**:11541–6.

Goebel M-O, Bachman J, Reichstein M *et al.* Soil water repellency and its implications for organic matter decomposition—is there a link to extreme climatic events?. *Glob Chang Biol* 2011;**17**:2640–56.

Gomez S, Bureau L, John K *et al.* Substrate stiffness impacts early biofilm formation by modulating *Pseudomonas aeruginosa* twitching motility. *eLife* 2023;**12**. https://doi.org/10.7554/eLife.81112.

Gomez-Arango LF, Barrett HL, McIntyre HD *et al.* Contributions of the maternal oral and gut microbiome to placental microbial colonization in overweight and obese pregnant women. *Sci Rep* 2017;**7**. https://doi.org/10.1038/S41598-017-03066-4.

Gordon V, Bakhtiari L, Kovach K. From molecules to multispecies ecosystems: the roles of structure in bacterial biofilms. *Phys Biol* 2019;**16**:041001.

Griffin D, Quail G. Movement of bacteria in moist particulate systems. *Aust Jnl Of Bio Sci* 1968;**21**:579.

Gupta S, Schillaci M, Roessner U. Metabolomics as an emerging tool to study plant–microbe interactions. *Emerg Top Life Sci* 2022;**6**:175–83.

Gupta VVSR, Sharma AK. *Rhizosphere Biology: Interactions Between Microbes and Plants*. Singapore: Springer, 2021.

Guzman CE, Bereza-Malcolm LT, De Groef B *et al.* Presence of selected methanogens, fibrolytic bacteria, and proteobacteria in the gastrointestinal tract of neonatal dairy calves from birth to 72 hours. *PLoS ONE* 2015;**10**:e0133048.

Guzman CE, Wood JL, Egidi E *et al.* A pioneer calf foetus microbiome. *Sci Rep* 2020;**10**. https://doi.org/10.1038/s41598-020-74677-7.

Hachani A, Wood TE, Filloux A. Type VI secretion and anti-host effectors. *Curr Opin Microbiol* 2016;**29**:81–93.

Hagen LH, Brooke CG, Shaw CA *et al.* Proteome specialization of anaerobic fungi during ruminal degradation of recalcitrant plant fiber. *ISME J* 2021;**15**:421–34.

Hand VL, Lloyd JR, Vaughan DJ *et al.* Experimental studies of the influence of grain size, oxygen availability and organic carbon availability on bioclogging in porous media. *Environ Sci Technol* 2008;**42**:1485–91.

Harcombe WR, Riehl WJ, Dukovski I *et al.* Metabolic resource allocation in individual microbes determines ecosystem interactions and spatial dynamics. *Cell Rep* 2014;**7**:1104–15.

Haryono MAS, Law YY, Arumugam K *et al.* Recovery of high quality metagenome-assembled genomes from full-scale activated sludge microbial communities in a tropical climate using longitudinal metagenome sampling. *Front Microbiol* 2022;**13**. https://doi.org/10.3389/fmicb.2022.869135.

Hayashi Y, Ken'ichirou K, Mizuyama T. Changes in pore size distribution and hydraulic properties of forest soil resulting from structural development. *J Hydrol* 2006;**331**:85–102.

He D, Liu L, Zhang Z *et al.* Association between gut microbiota and longevity: a genetic correlation and mendelian randomization study. *BMC Microbiol* 2022;**22**. https://doi.org/10.1186/s12866-022-02703-x.

Heinken A, Basile A, Thiele I. Advances in constraint-based modelling of microbial communities. *Curr Opin Syst Biol* 2021;**27**:100346.

Heinken A, Hertel J, Acharya G *et al.* Genome-scale metabolic reconstruction of 7,302 human microorganisms for personalized medicine. *Nat Biotechnol* 2023;**41**:1320–31, https://doi.org/10.1038/s41587-022-01628-0.

Hemida Abd-Alla M, Ahmed Omar S, Karanxha S. The impact of pesticides on arbuscular mycorrhizal and nitrogen-fixing symbioses in legumes. *Appl Soil Ecol* 2000;**14**:191–200.

Henderson G, Cox F, Ganesh S *et al.* Rumen microbial community composition varies with diet and host, but a core microbiome is found across a wide geographical range. *Sci Rep* 2015;**5**:1–15.
Hepworth MR, Monticelli LA, Fung TC *et al.* Innate lymphoid cells regulate CD4+ T-cell responses to intestinal commensal bacteria. *Nature* 2013;**498**:113–7.
Herold M, Martínez Arbas S, Narayanasamy S *et al.* Integration of time-series meta-omics data reveals how microbial ecosystems respond to disturbance. *Nat Commun* 2020;**11**:5281.
Herrington DA, Hall RH, Losonsky G *et al.* Toxin, toxin-coregulated pili, and the toxR regulon are essential for *Vibrio cholerae* pathogenesis in humans. *J Exp Med* 1988;**168**:1487–92,
Heydorn A, Nielsen AT, Hentzer M *et al.* Quantification of biofilm structures by the novel computer program comstat. *Microbiology* 2000;**146**:2395–407.
Hill C, Guarner F, Reid G *et al.* The International Scientific Association for Probiotics and Prebiotics consensus statement on the scope and appropriate use of the term probiotic. *Nat Rev Gastroenterol Hepatol* 2014;**11**:506–14.
Hoang DM, Levy EI, Vandenplas Y. The impact of caesarean section on the infant gut microbiome. *Acta Paediatr* 2021;**110**:60–67.
Hol WHG, Garbeva P, Hordijk C *et al.* Non-random species loss in bacterial communities reduces antifungal volatile production. *Ecology* 2015;**96**:2042–8.
Holtappels D, Alfenas-Zerbini P, Koskella B. Drivers and consequences of bacteriophage host range. *FEMS Microbiol Rev* 2023;**47**. https://doi.org/10.1093/femsre/fuad038.
Hu X, Li S, Mu R *et al.* The rumen microbiota contributes to the development of mastitis in dairy cows. *Microbiol Spectr* 2022;**10**. https://doi.org/10.1128/spectrum.02512-21.
Huang R, Wang Y, Liu D *et al.* Long-read metagenomics of marine microbes reveals diversely expressed secondary metabolites. *Microbiol Spectr* 2023;**11**. https://doi.org/10.1128/spectrum.01501-23.
Hummel G, Woodruff K, Austin K *et al.* Late gestation maternal feed restriction decreases microbial diversity of the placenta while mineral supplementation improves richness of the fetal gut microbiome in cattle. *Animals* 2021;**11**:2219.
Hummel GL, Austin K, Cunningham-Hollinger HC. Comparing the maternal-fetal microbiome of humans and cattle: a translational assessment of the reproductive, placental, and fetal gut microbiomes. *Biol Reprod* 2022;**107**:371–81.
Hungate BA, Marks JC, Power ME *et al.* The functional significance of bacterial predators. *mBio* 2021;**12**. https://doi.org/10.1128/mBio.00466-21.
Huuki H, Tapio M, Mäntysaari P *et al.* Long-term effects of early-life rumen microbiota modulation on dairy cow production performance and methane emissions. *Front Microbiol* 2022;**13**. https://doi.org/10.3389/fmicb.2022.983823.
Hwang Y, Roux S, Coclet C *et al.* Viruses interact with hosts that span distantly related microbial domains in dense hydrothermal mats. *Nat Microbiol* 2023;**8**:946–57.
Indrio F, Gutierrez Castrellon P, Vandenplas Y *et al.* Health effects of infant formula supplemented with probiotics or synbiotics in infants and toddlers: systematic review with network meta-analysis. *Nutrients* 2022;**14**:5175. https://doi.org/10.3390/NU14235175.
Ivleva NP, Kubryk P, Niessner R. Raman microspectroscopy, surface-enhanced Raman scattering microspectroscopy, and stable-isotope Raman microspectroscopy for biofilm characterization. *Anal Bioanal Chem* 2017;**409**:4353–75.
Jackson RB, Mooney HA, Schulze ED. A global budget for fine root biomass, surface area, and nutrient contents. *Proc Natl Acad Sci USA* 1997;**94**:7362–6.
Jaglin M, Rhimi M, Philippe C *et al.* Indole, a signaling molecule produced by the gut microbiota, negatively impacts emotional behaviors in rats. *Front Neurosci* 2018;**12**. https://doi.org/10.3389/fnins.2018.00216.
Jandhyala SM, Talukdar R, Subramanyam C *et al.* Role of the normal gut microbiota. *World J Gastroenterol* 2015;**21**:8787–803.
Jansma J, El Aidy S. Understanding the host-microbe interactions using metabolic modeling. *Microbiome* 2021;**9**:16.
Jarrell KF, McBride MJ. The surprisingly diverse ways that prokaryotes move. *Nat Rev Microbiol* 2008;**6**:466–76.
Jian J, Liang X. One small RNA of *Fusarium graminearum* targets and silences CEBiP gene in common wheat. *Microorganisms* 2019;**7**:425, https://doi.org/10.3390/microorganisms7100425.
Jiang Z, Nero T, Mukherjee S *et al.* Searching for the secret of stickiness: how biofilms adhere to surfaces. *Front Microbiol* 2021;**12**. https://doi.org/10.3389/fmicb.2021.686793.
Jouffret V, Miotello G, Culotta K *et al.* Increasing the power of interpretation for soil metaproteomics data. *Microbiome* 2021;**9**:195.
Jun S-R, Wassenaar TM, Nookaew I *et al.* Diversity of *Pseudomonas* genomes, including populus-associated isolates, as revealed by comparative genome analysis. *Appl Environ Microb* 2016;**82**:375–83.
Kalirad A, Sommer RJ. The art of mechanistic modeling in biology. *Nat Comput Sci* 2022;**2**:72–3.
Kark S, Van Rensburg BJ. Ecotones: marginal or central areas of transition?. *Israel J Ecol Evol* 2006;**52**:29–53.
Karlsson I, Friberg H, Steinberg C *et al.* Fungicide effects on fungal community composition in the wheat phyllosphere. *PLoS ONE* 2014;**9**:e111786.
Kastl AJ, Terry NA, Wu GD *et al.* The structure and function of the human small intestinal microbiota: current understanding and future directions. *Cell Mol Gastroenterol Hepatol* 2020;**9**:33–45.
Kawasaki A, Dennis PG, Forstner C *et al.* Manipulating exudate composition from root apices shapes the microbiome throughout the root system. *Plant Physiol* 2021;**187**:2279–95.
Kawasaki A, Donn S, Ryan PR *et al.* Microbiome and exudates of the root and rhizosphere of *Brachypodium distachyon*, a model for wheat. *PLoS ONE* 2016;**11**:e0164533. https://doi.org/10.1371/journal.pone.0164533.
Kazemian N, Ramezankhani M, Sehgal A *et al.* The trans-kingdom battle between donor and recipient gut microbiome influences fecal microbiota transplantation outcome. *Sci Rep* 2020;**10**:18349.
Ke J, Wang B, Yoshikuni Y. Microbiome engineering: synthetic biology of plant-associated microbiomes in sustainable agriculture. *Trends Biotechnol* 2021;**39**:244–61.
Kennedy KM, de Goffau MC, Perez-Muñoz ME *et al.* Questioning the fetal microbiome illustrates pitfalls of low-biomass microbial studies. *Nature* 2023;**613**:639–49.
Khan S, Shahid M, Khan MS *et al.* Fungicide-tolerant plant growth-promoting rhizobacteria mitigate physiological disruption of white radish caused by fungicides used in the field cultivation. *Int J Environ Res Public Health* 2020;**17**:1–26.
Kim SH, Ramos SC, Valencia RA *et al.* Heat stress: effects on rumen microbes and host physiology, and strategies to alleviate the negative impacts on lactating dairy cows. *Front Microbiol* 2022;**13**. https://doi.org/10.3389/fmicb.2022.804562.
Kim SY, Yi DY. Analysis of the human breast milk microbiome and bacterial extracellular vesicles in healthy mothers. *Exp Mol Med* 2020;**52**:1288–97.
Klemm P, Schembri MA. Bacterial adhesins: function and structure. *Int J Med Microbiol* 2000;**290**:27–35.

Kline KA, Fälker S, Dahlberg S *et al.* Bacterial adhesins in host-microbe interactions. *Cell Host Microbe* 2009;**5**:580–92.
Klümper U, Riber L, Dechesne A *et al.* Broad host range plasmids can invade an unexpectedly diverse fraction of a soil bacterial community. *ISME J* 2015;**9**:934–45.
Koeppen K, Hampton TH, Jarek M *et al.* A novel mechanism of host-pathogen interaction through sRNA in bacterial outer membrane vesicles. *PLoS Pathog* 2016;**12**:e1005672. https://doi.org/10.1371/journal.ppat.1005672.
Kolodny O, Callahan BJ, Douglas AE. The role of the microbiome in host evolution. *Phil Trans R Soc B* 2020;**375**:20190588. https://doi.org/10.1098/rstb.2019.0588.
Kondejewski LH, Farmer SW, Wishart DS *et al.* Modulation of structure and antibacterial and hemolytic activity by ring size in cyclic Gramicidin S analogs*. *J Biol Chem* 1996;**271**:25261–8.
Koskella B, Taylor TB. Multifaceted impacts of bacteriophages in the plant microbiome. *Annu Rev Phytopathol* 2018;**56**:361–80.
Krogstad KC, Bradford BJ. Does feeding starch contribute to the risk of systemic inflammation in dairy cattle?. *JDS Commun* 2023;**4**:14–18.
Labavić D, Loverdo C, Bitbol A-F Hydrodynamic flow and concentration gradients in the gut enhance neutral bacterial diversity. *Proc Natl Acad Sci USA* 2022;**119**. https://doi.org/10.1073/pnas.2108671119.
Langford FM, Weary DM, Fisher L. Antibiotic resistance in gut bacteria from dairy calves: a dose response to the level of antibiotics fed in milk. *J Dairy Sci* 2003;**86**:3963–6.
Law SR, Serrano AR, Daguerre Y *et al.* Metatranscriptomics captures dynamic shifts in mycorrhizal coordination in boreal forests. *Proc Natl Acad Sci USA* 2022;**119**:e2118852119.
Lee KWK, Periasamy S, Mukherjee M *et al.* Biofilm development and enhanced stress resistance of a model, mixed-species community biofilm. *ISME J* 2014;**8**:894–907.
Leng RA. Biofilm compartmentalisation of the rumen microbiome: modification of fermentation and degradation of dietary toxins. *Anim Prod Sci* 2017;**57**:2188.
Lennon JT, Jones SE. Microbial seed banks: the ecological and evolutionary implications of dormancy. *Nat Rev Micro* 2011;**9**:119–30.
Li F, Shah AM, Wang Z *et al.* Effects of land transport stress on variations in ruminal microbe diversity and immune functions in different breeds of cattle. *Animals* 2019;**9**:599.
Li J, Wu C, Chen S *et al.* Enriching indigenous microbial consortia as a promising strategy for xenobiotics' cleanup. *J Clean Prod* 2020;**261**:121234.
Li K, Shi B, Na R. The colonization of rumen microbiota and intervention in pre-weaned ruminants. *Animals* 2023;**13**:994.
Li W, Tapiainen T, Brinkac L *et al.* Vertical transmission of gut microbiome and antimicrobial resistance genes in infants exposed to antibiotics at birth. *J Infect Dis* 2021;**224**:1236.
Liu S, Zhang Z, Ma L. A review focusing on microbial vertical transmission during sow pregnancy. *Vet Sci* 2023;**10**:123. https://doi.org/10.3390/VETSCI10020123.
Liu W, Røder HL, Madsen JS *et al.* Interspecific bacterial interactions are reflected in multispecies biofilm spatial organization. *Front Microbiol* 2016;**7**. https://doi.org/10.3389/fmicb.2016.01366.
Logan SL, Thomas J, Yan J *et al.* The *Vibrio cholerae* type VI secretion system can modulate host intestinal mechanics to displace gut bacterial symbionts. *Proc Natl Acad Sci USA* 2018;**115**. https://doi.org/10.1073/pnas.1720133115.
Loh ZH, Ouwerkerk D, Klieve AV *et al.* Toxin degradation by rumen microorganisms: a review. *Toxins* 2020;**12**:664.
Long G, Hu Y, Tao E *et al.* The influence of cesarean section on the composition and development of gut microbiota during the first 3 months of life. *Front Microbiol* 2021;**12**:691312.
Lopes LD, Hao J, Schachtman DP. Alkaline soil pH affects bulk soil, rhizosphere and root endosphere microbiomes of plants growing in a Sandhills ecosystem. *FEMS Microbiol Ecol* 2021;**97**. https://doi.org/10.1093/femsec/fiab028.
Lovley DR, Coates JD, Blunt-Harris EL *et al.* Humic substances as electron acceptors for microbial respiration. *Nature* 1996;**382**:445–8.
Low CX, Tan LTH, Mutalib NSA *et al.* Unveiling the impact of antibiotics and alternative methods for animal husbandry: a review. *Antibiotics* 2021;**10**:578. https://doi.org/10.3390/ANTIBIOTICS10050578.
Ma J, Li Z, Zhang W *et al.* Comparison of gut microbiota in exclusively breast-fed and formula-fed babies: a study of 91 term infants. *Sci Rep* 2020;**10**:1–11.
Macfarlane S, Bahrami B, Macfarlane GT. Mucosal biofilm communities in the human intestinal tract. *Adv Appl Microbiol* 2011;**75**:111–43.
Macfarlane S, Macfarlane GT. Composition and metabolic activities of bacterial biofilms colonizing food residues in the human gut. *Appl Environ Microb* 2006;**72**:6204–11.
Malmuthuge N, Li M, Goonewardene LA *et al.* Effect of calf starter feeding on gut microbial diversity and expression of genes involved in host immune responses and tight junctions in dairy calves during weaning transition. *J Dairy Sci* 2013;**96**:3189–200.
Martín-Peláez S, Cano-Ibáñez N, Pinto-Gallardo M *et al.* The impact of probiotics, prebiotics, and synbiotics during pregnancy or lactation on the intestinal microbiota of children born by cesarean section: a systematic review. *Nutrients* 2022;**14**:341.
Martins SJ, Taerum SJ, Triplett L *et al.* Predators of soil bacteria in plant and human health. *Phytobiomes J* 2022;**6**:184–200.
Masood S, Bano A. Mechanism of potassium solubilization in the agricultural soils by the help of soil microorganisms. In: Meena V, Maurya B, Verma J *et al.* (eds.), *Potassium Solubilizing Microorganisms for Sustainable Agriculture*. New Delhi: Springer, 2016, 137–47.
Massalha H, Korenblum E, Malitsky S *et al.* Live imaging of root–bacteria interactions in a microfluidics setup. *Proc Natl Acad Sci USA* 2017;**114**:4549–54.
Mathes F, Murugaraj P, Bougoure J *et al.* Engineering rhizobacterial community resilience with mannose nanofibril hydrogels towards maintaining grain production under drying climate stress. *Soil Biol Biochem* 2020;**142**:107715.
Matz C, Kjelleberg S. Off the hook—how bacteria survive protozoan grazing. *Trends Microbiol* 2005;**13**:302–7.
McAllister TA, Bae HD, Jones GA *et al.* Microbial attachment and feed digestion in the rumen. *J Anim Sci* 1994;**72**:3004–18.
Mendes R, Raaijmakers JM. Cross-kingdom similarities in microbiome functions. *ISME J* 2015;**9**:1905–7.
Meyer-Dombard DR, Swingley W, Raymond J *et al.* Hydrothermal ecotones and streamer biofilm communities in the Lower Geyser Basin, Yellowstone National Park. *Environ Microbiol* 2011;**13**:2216–31.
Milani C, Duranti S, Bottacini F *et al.* The first microbial colonizers of the human gut: composition, activities, and health implications of the infant gut microbiota. *Microbiol Mol Biol Rev* 2017;**81**. https://doi.org/10.1128/MMBR.00036-17.
Mills AL. Keeping in touch: microbial life on soil particle surfaces. *Adv Agron* 2003;**78**:1–43.
Miron J, Ben-Ghedalia D, Morrison M. Invited review: adhesion mechanisms of rumen cellulolytic bacteria. *J Dairy Sci* 2001;**84**:1294–309.

Monteiro HF, Zhou Z, Gomes MS *et al.* Rumen and lower gut microbiomes relationship with feed efficiency and production traits throughout the lactation of Holstein dairy cows. *Sci Rep* 2022;**12**:1–14.

Moore MR, Schrag SJ, Schuchat A. Effects of intrapartum antimicrobial prophylaxis for prevention of group-B-streptococcal disease on the incidence and ecology of early-onset neonatal sepsis. *Lancet Infect Dis* 2003;**3**:201–13.

Morais LH, Schreiber HL, Mazmanian SK. The gut microbiota–brain axis in behaviour and brain disorders. *Nat Rev Micro* 2021;**19**: 241–55.

Moraïs S, Mizrahi I. The road not taken: the rumen microbiome, functional groups, and community states. *Trends Microbiol* 2019;**27**:538–49.

Moran NA, Ochman H, Hammer TJ. Evolutionary and ecological consequences of gut microbial communities. *Annu Rev Ecol Evol Syst* 2019;**50**:451–75.

Moroenyane I, Tremblay J, Yergeau E. Soybean microbiome recovery after disruption is modulated by the seed and not the soil microbiome. *Phytobiomes J* 2021;**5**:418–31.

Mueller NT, Differding MK, Sun H *et al.* Maternal bacterial engraftment in multiple body sites of cesarean section born neonates after vaginal seeding—a randomized controlled trial. *mBio* 2023;**14**. https://doi.org/10.1128/mbio.00491-23.

Muhammad MH, Idris AL, Fan X *et al.* Beyond risk: bacterial biofilms and their regulating approaches. *Front Microbiol* 2020;**11**. https://doi.org/10.3389/fmicb.2020.00928.

Muok AR, Claessen D, Briegel A. Microbial hitchhiking: how Streptomyces spores are transported by motile soil bacteria. *ISME J* 2021;**15**:2591–600.

Nadeem SM, Zahir ZA, Naveed M *et al.* Preliminary investigations on inducing salt tolerance in maize through inoculation with rhizobacteria containing ACC deaminase activity. *Can J Microbiol* 2007;**53**:1141–9.

Nagarajan K, Ni C, Lu T. Agent-based modeling of microbial communities. *ACS Synth Biol* 2022;**11**:3564–74.

Naiman RJ, Décamps H. The ecology of interfaces: riparian zones *Ann Rev Ecol Syst* 1997;**28**. https://doi.org/10.1146/annurev.ecolsys.28.1.621.

Nealson KH, Finkel SE. Electron flow and biofilms. *MRS Bull* 2011;**36**:380–4.

Nearing JT, Comeau AM, Langille MGI. Identifying biases and their potential solutions in human microbiome studies. *Microbiome* 2021;**9**:113.

Neubauer V, Petri RM, Humer E *et al.* Starch-rich diet induced rumen acidosis and hindgut dysbiosis in dairy cows of different lactations. *Animals* 2020;**10**:1727.

Newbold CJ, Ramos-Morales E. Review: ruminal microbiome and microbial metabolome: effects of diet and ruminant host. *Animal* 2020;**14**:s78–86.

Niu B, Paulson JN, Zheng X *et al.* Simplified and representative bacterial community of maize roots. *Proc Natl Acad Sci USA* 2017;**114**. https://doi.org/10.1073/pnas.1616148114.

Nuccio EE, Blazewicz SJ, Lafler M *et al.* HT-SIP: a semi-automated stable isotope probing pipeline identifies cross-kingdom interactions in the hyphosphere of arbuscular mycorrhizal fungi. *Microbiome* 2022;**10**:199.

O'Hara E, Neves ALA, Song Y *et al.* The role of the gut microbiome in cattle production and health: driver or passenger?. *Annu Rev Anim Biosci* 2020;**8**:199–220.

Oliveira NM, Wheeler JHR, Deroy C *et al.* Suicidal chemotaxis in bacteria. *Nat Commun* 2022;**13**:1–14.

Palestrant D, Holzknecht ZE, Collins BH *et al.* Microbial biofilms in the gut: visualization by electron microscopy and by acridine orange staining. *Ultrastruct Pathol* 2004;**28**:23–27.

Palmer J, Flint S, Brooks J. Bacterial cell attachment, the beginning of a biofilm. *J Ind Microbiol Biotechnol* 2007;**34**:577–88.

Pannaraj PS, Li F, Cerini C *et al.* Association between breast milk bacterial communities and establishment and development of the infant gut microbiome. *JAMA Pediatr* 2017;**171**:647.

Pereira RVV, Carroll LM, Lima S *et al.* Impacts of feeding preweaned calves milk containing drug residues on the functional profile of the fecal microbiota OPEN. *Sci Rep* 2018;**8**. https://doi.org/10.1038/s41598-017-19021-2.

Perez-Pardo P, Dodiya HB, Engen PA *et al.* Role of TLR4 in the gut-brain axis in Parkinson's disease: a translational study from men to mice. *Gut* 2019;**68**:829–43.

Pham VTH, Murugaraj P, Mathes F *et al.* Copolymers enhance selective bacterial community colonization for potential root zone applications. *Sci Rep* 2017;**7**:15902.

Pieterse CMJ, Van Wees SCM, Van Pelt JA *et al.* A novel signaling pathway controlling induced systemic resistance in *Arabidopsis*. *Plant Cell* 1998;**10**:1571–80.

Pinnell LJ, Reyes AA, Wolfe CA *et al.* Bacteroidetes and Firmicutes drive differing microbial diversity and community composition among micro-environments in the bovine rumen. *Front Vet Sci* 2022;**9**. https://doi.org/10.3389/fvets.2022.897996.

Plett JM, Daguerre Y, Wittulsky S *et al.* Effector MiSSP7 of the mutualistic fungus Laccaria bicolor stabilizes the Populus JAZ6 protein and represses jasmonic acid (JA) responsive genes. *Proc Natl Acad Sci USA* 2014;**111**:8299–304.

Pozo MJ, Cordier C, Dumas-Gaudot E *et al.* Localized versus systemic effect of arbuscular mycorrhizal fungi on defence responses to Phytophthora infection in tomato plants. *J Exp Bot* 2002;**53**: 525–34.

Pozo MJ, Van Der Ent S, Van Loon LC *et al.* Transcription factor MYC2 is involved in priming for enhanced defense during rhizobacteria-induced systemic resistance in *Arabidopsis thaliana*. *New Phytol* 2008;**180**:511–23.

Price ND, Reed JL, Palsson BØ. Genome-scale models of microbial cells: evaluating the consequences of constraints. *Nat Rev Micro* 2004;**2**:886–97.

Qian Y, Lan F, Venturelli OS. Towards a deeper understanding of microbial communities: integrating experimental data with dynamic models. *Curr Opin Microbiol* 2021;**62**:84–92.

Qiao Q, Wang F, Zhang J *et al.* The variation in the rhizosphere microbiome of cotton with soil type, genotype and developmental stage. *Sci Rep* 2017;**7**:3940.

Queck S-Y, Weitere M, Moreno AM *et al.* The role of quorum sensing mediated developmental traits in the resistance of *Serratia marcescens* biofilms against protozoan grazing. *Environ Microbiol* 2006;**8**:1017–25.

Rada V, Vlková E, Nevoral J *et al.* Comparison of bacterial flora and enzymatic activity in faeces of infants and calves. *FEMS Microbiol Lett* 2006;**258**:25–28.

Rajagopala SV, Bakhoum NG, Pakala SB *et al.* Metatranscriptomics to characterize respiratory virome, microbiome, and host response directly from clinical samples. *Cell Rep Methods* 2021;**1**:100091.

Ramayo-Caldas Y, Zingaretti L, Popova M *et al.* Identification of rumen microbial biomarkers linked to methane emission in Holstein dairy cows. *J Anim Breed Genet* 2020;**137**:49–59.

Ramírez-Puebla ST, Servín-Garcidueñas LE, Jiménez-Marín B *et al.* Gut and root microbiota commonalities. *Appl Environ Microb* 2013;**79**:2–9.

Raymond J, Alsop EB. Microbial evolution in extreme environments: microbial migration, genomic highways, and geochemical barriers in hydrothermal ecosystems. *Environ Syst Res* 2015;**4**. https://doi.org/10.1186/s40068-015-0038-x.

Rea MC, Dobson A, O'Sullivan O *et al.* Effect of broad- and narrow-spectrum antimicrobials on *Clostridium difficile* and microbial diversity in a model of the distal colon. *Proc Natl Acad Sci USA* 2011;**108**:4639–44.

Regmi R, Newman TE, Kamphuis LG *et al.* Identification of *B. napus* small RNAs responsive to infection by a necrotrophic pathogen. *BMC Plant Biol* 2021;**21**. https://doi.org/10.1186/s12870-021-03148-6.

Regmi R, Penton CR, Anderson J *et al.* Do small RNAs unlock the below ground microbiome-plant interaction mystery?. *Front Mol Biosci* 2022;**9**.1017392

Ren B, Wang X, Duan J *et al.* Rhizobial TRNA-derived small RNAs are signal molecules regulating plant nodulation. *Science* 2019;**365**:919–22.

Rendueles O, Ghigo J-M. Mechanisms of competition in biofilm communities. *Microbiol Spectr* 2015;**3**. https://doi.org/10.1128/microbiolspec.MB-0009-2014.

Renner LD, Weibel DB. Physicochemical regulation of biofilm formation. *MRS Bull* 2011;**36**:347–55.

Reyman M, van Houten MA, van Baarle D *et al.* Impact of delivery mode-associated gut microbiota dynamics on health in the first year of life. *Nat Commun* 2019;**10**:4997. https://doi.org/10.1038/s41467-019-13014-7.

Ritpitakphong U, Falquet L, Vimoltust A *et al.* The microbiome of the leaf surface of *Arabidopsis* protects against a fungal pathogen. *New Phytol* 2016;**210**:1033–43.

Rodionov DA, Arzamasov AA, Khoroshkin MS *et al.* Micronutrient requirements and sharing capabilities of the human gut microbiome. *Front Microbiol* 2019;**10**. https://doi.org/10.3389/fmicb.2019.01316.

Rodríguez-Ramos JA, Borton MA, McGivern BB *et al.* Genome-resolved metaproteomics decodes the microbial and viral contributions to coupled carbon and nitrogen cycling in river sediments. *mSystems* 2022;**7**. https://doi.org/10.1128/msystems.00516-22.

Rogers AP, Mileto SJ, Lyras D. Impact of enteric bacterial infections at and beyond the epithelial barrier. *Nat Rev Micro* 2023;**21**:260–74.

Rohart F, Gautier B, Singh A *et al.* mixOmics: an R package for 'omics feature selection and multiple data integration. *PLoS Comput Biol* 2017;**13**:e1005752.

Ronda C, Chen SP, Cabral V *et al.* Metagenomic engineering of the mammalian gut microbiome in situ. *Nat Methods* 2019;**16**:167–70.

Ruan W, Engevik MA, Spinler JK *et al.* Healthy human gastrointestinal microbiome: composition and function after a decade of exploration. *Dig Dis Sci* 2020;**65**:695–705.

Rubin BE, Diamond S, Cress BF *et al.* Species- and site-specific genome editing in complex bacterial communities. *Nat Microbiol* 2022;**7**:34–47.

Rudrappa T, Biedrzycki ML, Bais HP. Causes and consequences of plant-associated biofilms. *FEMS Microbiol Ecol* 2008;**64**:153–66.

Ruppert KG, Matthew C, McKenzie CM *et al.* Impact of Epichloë endophytes on adult Argentine stem weevil damage to perennial ryegrass seedlings. *Entomologia Exp Applicata* 2017;**163**:328–37.

Russell JB, Muck RE, Weimer PJ. Quantitative analysis of cellulose degradation and growth of cellulolytic bacteria in the rumen. *FEMS Microbiol Ecol* 2009;**67**:183–97.

Ryu CM, Farag MA, Hu CH *et al.* Bacterial volatiles induce systemic resistance in *Arabidopsis*. *Plant Physiol* 2004;**134**:1017–26.

Saarenpää S, Shalev O, Ashkenazy H *et al.* Spatial metatranscriptomics resolves host–bacteria–fungi interactomes. *Nat Biotechnol* 2023. https://www.nature.com/articles/s41587-023-01979-2.

Sadiq FA, Burmølle M, Heyndrickx M *et al.* Community-wide changes reflecting bacterial interspecific interactions in multispecies biofilms. *Crit Rev Microbiol* 2021;**47**:338–58.

Sahr T, Escoll P, Rusniok C *et al.* Translocated *Legionella pneumophila* small RNAs mimic eukaryotic microRNAs targeting the host immune response. *Nat Commun* 2022;**13**. https://doi.org/10.1038/s41467-022-28454-x.

Salem H, Bauer E, Strauss AS *et al.* Vitamin supplementation by gut symbionts ensures metabolic homeostasis in an insect host. *Proc R Soc B* 2014;**281**:20141838. https://doi.org/10.1098/rspb.2014.1838.

Sanjorjo RA, Tseten T, Kang M-K *et al.* In pursuit of understanding the rumen microbiome. *Fermentation* 2023;**9**:114.

Santhanam R, Luu VT, Weinhold A *et al.* Native root-associated bacteria rescue a plant from a sudden-wilt disease that emerged during continuous cropping. *Proc Natl Acad Sci USA* 2015;**112**:E5013–120.

Sasson G, Moraïs S, Kokou F *et al.* Metaproteome plasticity sheds light on the ecology of the rumen microbiome and its connection to host traits. *ISME J* 2022;**16**:2610–21.

Schulz-Bohm K, Gerards S, Hundscheid M *et al.* Calling from distance: attraction of soil bacteria by plant root volatiles. *ISME J* 2018;**12**:1252–62.

Seaver SMD, Lerma-Ortiz C, Conrad N *et al.* PlantSEED enables automated annotation and reconstruction of plant primary metabolism with improved compartmentalization and comparative consistency. *Plant J* 2018;**95**:1102–13.

Seaver SMD, Liu F, Zhang Q *et al.* The ModelSEED Biochemistry Database for the integration of metabolic annotations and the reconstruction, comparison and analysis of metabolic models for plants, fungi and microbes. *Nucleic Acids Res* 2021;**49**:D575–88.

Sentenac H, Loyau A, Leflaive J *et al.* The significance of biofilms to human, animal, plant and ecosystem health. *Funct Ecol* 2022;**36**:294–313.

Sequeira RP, McDonald JAK, Marchesi JR *et al.* Commensal Bacteroidetes protect against *Klebsiella pneumoniae* colonization and transmission through IL-36 signalling. *Nat Microbiol* 2020;**5**:304–13.

Sereika M, Petriglieri F, Jensen TBN *et al.* Closed genomes uncover a saltwater species of *Candidatus* Electronema and shed new light on the boundary between marine and freshwater cable bacteria. *ISME J* 2023;**17**:561–9.

Sharon G, Segal D, Ringo JM *et al.* Commensal bacteria play a role in mating preference of *Drosophila melanogaster*. *Proc Natl Acad Sci USA* 2010;**107**:20051–6.

Shi H, Grodner B, De Vlaminck I. Recent advances in tools to map the microbiome. *Curr Opin Biomed Eng* 2021;**19**:100289.

Shi H, Shi Q, Grodner B *et al.* Highly multiplexed spatial mapping of microbial communities. *Nature* 2020;**588**:676–81.

Shi J, Lei Y, Wu J *et al.* Antimicrobial peptides act on the rumen microbiome and metabolome affecting the performance of castrated bulls. *J Anim Sci Biotechnol* 2023;**14**. https://doi.org/10.1186/s40104-023-00832-5.

Shi L, Dong H, Reguera G *et al.* Extracellular electron transfer mechanisms between microorganisms and minerals. *Nat Rev Micro* 2016;**14**:651–62.

Shi S, Nuccio E, Herman DJ *et al.* Successional trajectories of rhizosphere bacterial communities over consecutive seasons. *mBio* 2015;**6**. https://doi.org/10.1128/mBio.00746-15.

Shoaie S, Ghaffari P, Kovatcheva-Datchary P *et al.* Quantifying diet-induced metabolic changes of the human gut microbiome. *Cell Metab* 2015;**22**:320–31.

Silvestri A, Turina M, Fiorilli V *et al.* Different genetic sources contribute to the small RNA population in the arbuscular mycorrhizal fungus *Gigaspora margarita*. *Front Microbiol* 2020;**11**. https://doi.org/10.3389/fmicb.2020.00395.

Singh BK, Yan ZZ, Whittaker M *et al.* Soil microbiomes must be explicitly included in One Health policy. *Nat Microbiol* 2023;**8**:1367–72. https://doi.org/10.1038/s41564-023-01386-y.

Sola-Leyva A, Andrés-León E, Molina NM *et al.* Mapping the entire functionally active endometrial microbiota. *Hum Reprod* 2021;**36**:1021–31.

Solís-García IA, Ceballos-Luna O, Cortazar-Murillo EM *et al.* Phytophthora root rot modifies the composition of the avocado rhizosphere microbiome and increases the abundance of opportunistic fungal pathogens. *Front Microbiol* 2021;**11**. https://doi.org/10.3389/fmicb.2020.574110.

Solomon R, Wein T, Levy B *et al.* Protozoa populations are ecosystem engineers that shape prokaryotic community structure and function of the rumen microbial ecosystem. *ISME J* 2022;**16**:1187–97.

Soria-Bustos J, Ares MA, Gómez-Aldapa CA *et al.* Two type VI secretion systems of enterobacter cloacae are required for bacterial competition, cell adherence, and intestinal colonization. *Front Microbiol* 2020;**11**. https://doi.org/10.3389/fmicb.2020.560488.

Stergiadis S, Cabeza-Luna I, Mora-Ortiz M *et al.* Unravelling the role of rumen microbial communities, genes, and activities on milk fatty acid profile using a combination of omics approaches. *Front Microbiol* 2021;**11**:3540.

Stewart CJ, Ajami NJ, O'Brien JL *et al.* Temporal development of the gut microbiome in early childhood from the TEDDY study. *Nature* 2018;**562**:583–8.

Stinson LF, Boyce MC, Payne MS *et al.* The not-so-sterile womb: Evidence that the human fetus is exposed to bacteria prior to birth. *Front Microbiol* 2019;**10**. https://doi.org/10.3389/FMICB.2019.01124/PDF.

Strandwitz P, Kim KH, Terekhova D *et al.* GABA-modulating bacteria of the human gut microbiota. *Nat Microbiol* 2019;**4**:396–403.

Swamy MK, MohdS A, Sinniah UR. Root exudates and their molecular interactions with rhizospheric microbes. In: *Plant, Soil and Microbes* Cham: Springer International Publishing. 2016, 59–77.

Tamburini S, Shen N, Wu HC *et al.* The microbiome in early life: implications for health outcomes. *Nat Med* 2016;**22**:713–22.

Tan MSF, White AP, Rahman S *et al.* Role of fimbriae, flagella and cellulose on the attachment of *Salmonella* Typhimurium ATCC 14028 to plant cell wall models. *PLoS ONE* 2016;**11**:e0158311.

Tao F, Huang Y, Hungate BA *et al.* Microbial carbon use efficiency promotes global soil carbon storage. *Nature* 2023;**618**:981–5.

Thiele I, Swainston N, Fleming RMT *et al.* A community-driven global reconstruction of human metabolism. *Nat Biotechnol* 2013;**31**:419–25.

Thompson JA, Oliveira RA, Djukovic A *et al.* Manipulation of the quorum sensing signal AI-2 affects the antibiotic-treated gut microbiota. *Cell Rep* 2015;**10**:1861–71.

Thormann KM, Saville RM, Shukla S *et al.* Induction of Rapid Detachment in *Shewanella oneidensis* MR-1 Biofilms. *J Bacteriol* 2005;**187**:1014–21.

Thursby E, Juge N. Introduction to the human gut microbiota. *Biochem J* 2017;**474**:1823–36.

Tiedje JM, Bruns MA, Casadevall A *et al.* Microbes and climate change: a research prospectus for the future. *mBio* 2022;**13**. https://doi.org/10.1128/mbio.00800-22.

Tiezzi F, Fix J, Schwab C *et al.* Gut microbiome mediates host genomic effects on phenotypes: a case study with fat deposition in pigs. *Comput Struct Biotechnol J* 2021;**19**:530–44.

Tkacz A, Cheema J, Chandra G *et al.* Stability and succession of the rhizosphere microbiota depends upon plant type and soil composition. *ISME J* 2015;**9**:2349–59.

Toju H, Peay KG, Yamamichi M *et al.* Core microbiomes for sustainable agroecosystems. *Nat Plants* 2018;**4**:247–57.

Tomlinson AD, Fuqua C. Mechanisms and regulation of polar surface attachment in *Agrobacterium tumefaciens*. *Curr Opin Microbiol* 2009;**12**:708–14.

Toyofuku M, Inaba T, Kiyokawa T *et al.* Environmental factors that shape biofilm formation. *Biosci Biotechnol Biochem* 2016;**80**:7–12.

Tripathi A, Debelius J, Brenner DA *et al.* The gut-liver axis and the intersection with the microbiome. *Nat Rev Gastroenterol Hepatol* 2018;**15**:397–411.

Trivedi P, Leach JE, Tringe SG *et al.* Plant–microbiome interactions: from community assembly to plant health. *Nat Rev Micro* 2020;**18**:607–21.

Truyens S, Weyens N, Cuypers A *et al.* Bacterial seed endophytes: genera, vertical transmission and interaction with plants. *Environ Microbiol Rep* 2015;**7**:40–50.

Tytgat HLP, Nobrega FL, van der Oost J *et al.* Bowel biofilms: tipping points between a healthy and compromised gut?. *Trends Microbiol* 2019;**27**:17–25.

UNICEF. *Breastfeeding: A Mother's Gift, for Every Child*. New York, 2018.

Urban J, Čermák J, Ceulemans R. Above- and below-ground biomass, surface and volume, and stored water in a mature Scots pine stand. *Eur J Forest Res* 2015;**134**:61–74.

Ursell LK, Metcalf JL, Parfrey LW *et al.* Defining the human microbiome. *Nutr Rev* 2012;**70**:S38–44.

van den Berg NI, Machado D, Santos S *et al.* Ecological modelling approaches for predicting emergent properties in microbial communities. *Nat Ecol Evol* 2022;**6**:855–65.

van der Heijden MGA, Martin FM, Selosse MA *et al.* Mycorrhizal ecology and evolution: the past, the present, and the future. *New Phytol* 2015;**205**:1406–23.

van Elsas JD, Semenov AV, Costa R *et al.* Survival of *Escherichia coli* in the environment: fundamental and public health aspects. *ISME J* 2011;**5**:173–83.

Van Goethem MW, Osborn AR, Bowen BP *et al.* Long-read metagenomics of soil communities reveals phylum-specific secondary metabolite dynamics. *Commun Biol* 2021;**4**:1302.

Vatanen T, Plichta DR, Somani J *et al.* Genomic variation and strain-specific functional adaptation in the human gut microbiome during early life. *Nat Microbiol* 2018;**4**:470–9.

Velten B, Braunger JM, Argelaguet R *et al.* Identifying temporal and spatial patterns of variation from multimodal data using MEFISTO. *Nat Methods* 2022;**19**:179–86.

Ventura M, Turroni F, Motherway MO *et al.* Host–microbe interactions that facilitate gut colonization by commensal bifidobacteria. *Trends Microbiol* 2012;**20**:467–76.

Venturelli OS, Carr AV, Fisher G *et al.* Deciphering microbial interactions in synthetic human gut microbiome communities. *Mol Syst Biol* 2018;**14**. https://doi.org/10.15252/msb.20178157.

Vernocchi P, Del Chierico F, Putignani L. Gut microbiota profiling: metabolomics based approach to unravel compounds affecting human health. *Front Microbiol* 2016;**7**:1144.

Vesper SJ. Production of pili (fimbriae) by *Pseudomonas fluorescens* and correlation with attachment to corn roots. *Appl Environ Microb* 1987;**53**:1397–405.

Vlková E, Trojanová I, Rada V. Distribution of bifidobacteria in the gastrointestinal tract of calves. *Folia Microbiol* 2006;**51**: 25–8.

Walker WA. The importance of appropriate initial bacterial colonization of the intestine in newborn, child, and adult health. *Pediatr Res* 2017;**82**:387–95.

Wang BX, Wu CM, Ribbeck K. Home, sweet home: how mucus accommodates our microbiota. *FEBS J* 2021a;**288**:1789–99.

Wang C, Li Y, Li M *et al.* Functional assembly of root-associated microbial consortia improves nutrient efficiency and yield in soybean. *JIPB* 2021b;**63**:1021–35.

Wang H, Liu R, You MP *et al.* Pathogen biocontrol using plant growth-promoting bacteria (PGPR): role of bacterial diversity. *Microorganisms* 2021c;**9**:1988.

Wang J, Li Z, Ma X *et al.* Translocation of vaginal microbiota is involved in impairment and protection of uterine health. *Nat Commun* 2021d;**12**. https://doi.org/10.1038/s41467-021-24516-8.

Wang M, Weiberg A, Dellota E *et al.* Botrytis small RNA Bc-siR37 suppresses plant defense genes by cross-kingdom RNAi. *RNA Biol* 2017a;**14**:421–8.

Wang Z, Elekwachi CO, Jiao J *et al.* Investigation and manipulation of metabolically active methanogen community composition during rumen development in black goats. *Sci Rep* 2017b;**7**: 422.

Wang S, Ryan CA, Boyaval P *et al.* Maternal vertical transmission affecting early-life microbiota development. *Trends Microbiol* 2020;**28**:28–45.

Watters C, Fleming D, Bishop D *et al.* Host responses to biofilm. *Prog Mol Biol Transl Sci* 2016;**142**:193–239.

Weiberg A, Wang M, Lin F *et al.* Fungal small RNAs suppress plant immunity by hijacking host RNA interference pathways. *Science* 2013;**342**:118–23.

Weinstein S, Wallace BA, Morrow JS *et al.* Conformation of the Gramicidin A transmembrane channel: a 13C nuclear magnetic resonance study of 13C-enriched gramicidin in phosphatidylcholine vesicles. *J Mol Biol* 1980;**143**:1–19.

Welch CB, Lourenco JM, Davis DB *et al.* The impact of feed efficiency selection on the ruminal, cecal, and fecal microbiomes of Angus steers from a commercial feedlot. *J Anim Sci* 2020;**98**. https://doi.org/10.1093/jas/skaa230.

Wendel U. Assessing viability and stress tolerance of probiotics—a review. *Front Microbiol* 2022;**12**. https://doi.org/10.3389/fmicb.2021.818468.

Weng M, Walker WA. The role of gut microbiota in programming the immune phenotype. *J Dev Orig Health Dis* 2013;**4**:203–14.

Wheatley RM, Poole PS. Mechanisms of bacterial attachment to roots. *FEMS Microbiol Rev* 2018;**42**. https://doi.org/10.1093/femsre/fuy014.

Whipps JM. Carbon economy. In: Lynch JM (ed.), *The Rhizosphere*. Essex: John Wiley & Sons Ltd, 1990, 59–97.

Williams CL, Thomas BJ, McEwan NR *et al.* Rumen protozoa play a significant role in fungal predation and plant carbohydrate breakdown. *Front Microbiol* 2020;**11**. https://doi.org/10.3389/fmicb.2020.00720.

Wolf AB, Vos M, de Boer W *et al.* Impact of matric potential and pore size distribution on growth dynamics of filamentous and non-filamentous soil bacteria. *PLoS ONE* 2013;**8**:e83661.

Won M-Y, Oyama LB, Courtney SJ *et al.* Can rumen bacteria communicate to each other?. *Microbiome* 2020;**8**:23.

Wong LL, Mugunthan S, Kundukad B *et al.* Microbial biofilms are shaped by the constant dialogue between biological and physical forces in the extracellular matrix. *Environ Microbiol* 2023;**25**:199–208.

Wong-Rolle A, Dong Q, Zhu Y *et al.* Spatial meta-transcriptomics reveal associations of intratumor bacteria burden with lung cancer cells showing a distinct oncogenic signature. *J Immunother Cancer* 2022;**10**:e004698.

World Health Organization. Breastfeeding. Geneva, 2023.

Wu S, Liu J, Liu C *et al.* Quorum sensing for population-level control of bacteria and potential therapeutic applications. *Cell Mol Life Sci* 2020;**77**:1319–43.

Wu Y, Cai P, Jing X *et al.* Soil biofilm formation enhances microbial community diversity and metabolic activity. *Environ Int* 2019;**132**:105116.

Xiao E, Cui J, Sun W *et al.* Root microbiome assembly of As-hyperaccumulator *Pteris vittata* and its efficacy in arsenic requisition. *Environ Microbiol* 2021;**23**:1959–71.

Xiao L, Zhao F. Microbial transmission, colonisation and succession: from pregnancy to infancy. *Gut* 2023;**72**:772–86.

Xiong Q, Liu D, Zhang H *et al.* Quorum sensing signal autoinducer-2 promotes root colonization of *Bacillus velezensis* SQR9 by affecting biofilm formation and motility. *Appl Microbiol Biotechnol* 2020;**104**:7177–85.

Xu Q, Qiao Q, Gao Y *et al.* Gut microbiota and their role in health and metabolic disease of dairy cow. *Front Nutr* 2021;**8**. https://doi.org/10.3389/fnut.2021.701511.

Xue M-Y, Xie Y-Y, Zhong Y *et al.* Integrated meta-omics reveals new ruminal microbial features associated with feed efficiency in dairy cattle. *Microbiome* 2022;**10**:32.

Yan J, Bassler BL. Surviving as a community: antibiotic tolerance and persistence in bacterial biofilms. *Cell Host Microbe* 2019;**26**: 15–21.

Yáñez-Ruiz DR, Abecia L, Newbold CJ. Manipulating rumen microbiome and fermentation through interventions during early life: a review. *Front Microbiol* 2015;**6**. https://doi.org/10.3389/fmicb.2015.01133.

Yao MK, Désilets H, Charles MT *et al.* Effect of mycorrhization on the accumulation of rishitin and solavetivone in potato plantlets challenged with *Rhizoctonia solani*. *Mycorrhiza* 2003;**13**:333–6.

Ye Q, Shao X, Shen R *et al.* Changes in the human gut microbiota composition caused by *Helicobacter pylori* eradication therapy: a systematic review and meta-analysis. *Helicobacter* 2020;**25**. https://doi.org/10.1111/hel.12713.

Yin X, Ji S, Duan C *et al.* Dynamic change of fungal community in the gastrointestinal tract of growing lambs. *J Integr Agric* 2022;**21**:3314–28.

Young IM, Crawford JW. Interactions and self-organization in the soil-microbe complex. *Science* 2004;**304**:1634–7.

Yu K, Rodriguez M, Paul Z *et al.* Transfer of oral bacteria to the fetus during late gestation. *Sci Rep* 2021;**11**. https://doi.org/10.1038/s41598-020-80653-y.

Yuwono T, Handayani D, Soedarsono J. The role of osmotolerant rhizobacteria in rice growth under different drought conditions. *Aust J Agric Res* 2005;**56**:715–21.

Zaller JG, König N, Tiefenbacher A *et al.* Pesticide seed dressings can affect the activity of various soil organisms and reduce decomposition of plant material. *BMC Ecol* 2016;**16**:1–11.

Zhang C, Li L, Biying J *et al.* The effects of delivery mode on the gut microbiota and health: state of art. *Front Microbiol* 2021a;**12**:724449. https://doi.org/10.3389/fmicb.2021.724449.

Zhang Y, Choi SH, Nogoy KM *et al.* Review: the development of the gastrointestinal tract microbiota and intervention in neonatal ruminants. *Animal* 2021b;**15**:100316.

Zhang J, Wei L, Yang J *et al.* Probiotic consortia: reshaping the rhizospheric microbiome and its role in suppressing root-rot disease of panax notoginseng. *Front Microbiol* 2020;**11**. https://doi.org/10.3389/fmicb.2020.00701.

Zhang T, Mu Y, Zhang R *et al.* Responsive changes of rumen microbiome and metabolome in dairy cows with different susceptibility to subacute ruminal acidosis. *Anim Nutr* 2022;**8**:331–40.

Zhang Y, Gao X, Shen Z *et al.* Pre-colonization of PGPR triggers rhizosphere microbiota succession associated with crop yield enhancement. *Plant Soil* 2019;**439**:553–67.

Zhao C, Hu X, Bao L *et al.* Gut dysbiosis induces the development of mastitis through a reduction in host anti-inflammatory enzyme activity by endotoxemia. *Microbiome* 2022a;**10**:205.

Zhao C, Wang L, Ke S *et al.* Yak rumen microbiome elevates fiber degradation ability and alters rumen fermentation pattern to increase feed efficiency. *Anim Nutr* 2022b;**11**:201–14.

Zhu YG, Zhao Y, Zhu D *et al.* Soil biota, antimicrobial resistance and planetary health. *Environ Int* 2019;**131**:105059. https://doi.org/10.1016/j.envint.2019.105059.

Zong X, Fu J, Xu B *et al.* Interplay between gut microbiota and antimicrobial peptides. *Anim Nutr* 2020;**6**:389–96.

Received 26 July 2023; **revised** 12 February 2024; **accepted** 27 February 2024