


The ecosystem services of animal microbiomes

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Abstract

Microbiologists often evaluate microbial community dynamics by formulating functional hypotheses based on ecological processes. Indeed, many of the methods and terms currently used to describe animal microbiomes derive from ecology and evolutionary biology. As our understanding of the composition and functional dynamics of “the microbiome” grows, we increasingly refer to the host as an ecosystem within which microbial processes play out. Even so, an ecosystem service framework that extends to the context of the host has thus far been lacking. Here, we argue that ecosystem services are a useful framework with which to consider the value of microbes to their hosts. We discuss those “microbiome services” in the specific context of the mammalian gut, providing a context from which to develop new hypotheses and to evaluate microbial functions in future studies and novel systems.

KEYWORDS

ecosystem services, host–microbiome, microbial ecology, microbiome

1 | INTRODUCTION

Animals are inhabited by microbial communities that together are referred to as “the microbiome.” These microbiomes can provide both benefits and costs to their host. Here, we argue that the concept of ecosystem services is a useful framework within which to consider the value of microbes to their hosts in general, and specifically, provides a framework in which to begin to predict when microbes are most likely to offer “services” to their host in terms of health and reproductive fitness. Our work builds upon and extends recent work in which other investigators have productively borrowed ecological frameworks to understand microbiome composition and change (Cho & Blaser, 2012; Christian et al., 2015; Costello, Stagaman, Dethlefsen, Bohannan, & Relman, 2012; Fierer et al., 2012; Leser & Mølbak, 2009; McFall-Ngai et al., 2013; Relman, 2012; Stilling, Bordenstein, Dinan, & Cryan, 2014; Walter & Ley, 2011), but broadens this effort by considering ecosystem services.

The host–microbe system is a unique context in which to consider ecosystem services, in as much as the host is always under selection to extract more services from the microbes (and shape the microbes in such a way as to provide those services), while the microbes are under selection to extract more benefits from the host. Selection on the host favours variants of host genes associated with

greater host fitness. Those gene variants can be associated with host morphologies that favour microbiome services beneficial to the host, which in turn filters the lineages and species present in the host’s microbial community. As a key example, in herbivores that consume high proportions of dietary fibre, selection has favoured complex gut morphologies inhabited by microbial communities that are able to ferment dietary fibre. Such a scenario is highly dynamic, with selection on hosts favouring both host genes associated with certain microbial processes, as well as on the microbes that carry them out.

But to further complete the ecological analogy, the microbes are perpetually interacting with each other, often as competitors, or even as predators and prey. This system is complex, and it is this complexity that makes it both interesting and potentially informative for larger questions in ecology and evolution. Here, we discuss “microbiome services” in the specific context of mammalian guts. We provide a context from which to develop new hypotheses and to evaluate microbial functions in future studies and novel systems. Though focused on the gut microbiome, the concepts introduced here are sufficiently general to apply to other host “ecosystems” and to larger questions of symbiotic interactions.

Dispersal, diversification, environmental selection and drift have traditionally informed hypotheses about the composition of microbial communities (Costello et al., 2012; Vellend, 2010). While these

ecological processes provide a framework for understanding microbial membership (Costello et al., 2012), they do not address the interactions or exchanges that comprise the host–microbiome relationship. Other reviews have enumerated the services provided by environmental microorganisms (Bodelier, 2011; Lemanceau et al., 2015) or suggested that Vellend's ecological processes may impact host health by shaping microbial community composition and functionality (Costello et al., 2012; Martiny, Jones, Lennon, & Martiny, 2015). However, an ecosystem service framework that directly extends microbial functions to the context of the host has thus far been lacking.

A recent review highlighted several microbial characteristics (including beneficial functions such as the production of goods and antibiotics) as pitfalls to the application of classical ecological and evolutionary theory to microbiomes (Koskella, Hall, & Metcalf, 2017). It is important to note that, while the traditional ecosystem service perspective is useful, it also requires heavy adaptation to bring it fully to bear on host–microbe interactions. Here, we focus specifically on functions collectively performed by the microbiome, to remove the dependence on classification of individual members that has proven a stumbling block to other classical frameworks. We also invoke the model of the microbiome as an “ecosystem on a leash” (Foster, Schluter, Coyte, & Rakoff-Nahoum, 2017), which provides evolutionary grounding for host selection of microbial communities that provide beneficial services.

We first review Vellend's processes in the specific context of the gut to summarize the community ecology framework that has previously been adopted. We focus on hindgut fermenters, in which the bulk of the microbiome resides in the caecum and colon, although certainly, all four processes should proceed with similar effect in foregut fermenting hosts as well. We then develop a framework building on ecosystem ecology and the concept of ecosystem services, using the same categorical subheadings originally used to describe ecosystem services (Millennium Ecosystem Assessment, 2005). After explicitly drawing parallels between each microbiome service and its ecosystem service counterpart, we predict specific cases when microbiome services impact host fitness and identify cases when they are cultivated through specific host behaviours.

2 | ECOLOGICAL PROCESSES

With regard to the gut microbiome, diet, gut morphology and gut physiology together define the environment unique to each host ecosystem, and that environment shapes the traits of the microbiome. Figure 1 presents several features of the gut that influence the diversity and composition of the gut microbiome and, ultimately, its services. They are here summarized:

1. Dispersal includes factors that help or hinder the spread of species and is a central principle of biogeography. As applied to the gut microbiome, each meal provides an influx of microbes associated with the food itself, as well as biotic and abiotic features of

the environment. Several features of gastrointestinal physiology also affect microbial dispersal: for example, peristalsis moves ingesta (including microbes) down the length of the gut. The length or complexity of the gut is typically coupled to gut transit time; and one can predict that where dispersal rates (i.e., gut passage rates) are higher, the change in composition in the gut microbiome through time will also be higher. Indeed, previous studies have shown that lemurs with shorter gut lengths and transit times exhibit greater microbial and metagenomic variation compared to species with more complex guts and slower moving digesta (McKenney, O'Connell, Rodrigo, & Yoder, 2017; McKenney, Rodrigo, & Yoder, 2015).

2. Environmental selection favours specific functions and roles in a given system that are best adapted to specific environmental conditions (Martiny et al., 2015). An herbivorous diet, for example, selects for microbes that are specifically adept at digesting fibre (McKenney, Greene, Drea, & Yoder, 2017; McKenney, O'Connell et al., 2017; McKenney et al., 2015; Stevens & Hume, 1998). The morphology of the gut also influences which microbial species can survive, whether as a function of the relative availability of oxygen or other features, while stomach acidity acts as a restrictive filter that prevents many species from colonizing the intestines or caecum (Beasley, Koltz, Lambert, Fierer, & Dunn, 2015). Stomachs differ in the extent to which they prevent dispersal as a function of their acidity, which both varies among species and also differs during the lifetime of an individual animal. In addition, through the production of mucins, the host can actively alter the environment of the gut and which microbes are favoured.
3. Diversification of gut community members occurs over evolutionary time, whether in response to competition, novel niches, dispersal into new hosts, or other factors. Gut lineages also diversify in response to host diversification (Ley, Peterson, & Gordon, 2006; Toft & Andersson, 2010). However, in as much as bacterial evolution is rapid relative to the life expectancies of hosts, diversification may also happen on very short timescales within the lives of individual hosts.
4. Finally, drift comprises stochastic processes that contribute to community structure. Gut transit eliminates a portion of the community (comprising transient membership) with waste. Therefore, transit may increase the effects of drift by decreasing the relative abundance of specific species, because drift affects rare species more than common species.

More recently, community assembly has been added to the traditional framework for understanding the community development of the gut microbiome (Nemergut et al., 2013). Previous studies evaluating primary and secondary succession detected similar trends in diversity, with complexity increasing but interindividual variation decreasing as communities assemble over time (Figure 2). After birth, nursing infants initially exhibit high gut microbial variation; but diet predictably shapes community structure, and convergence towards stable adult climax communities is

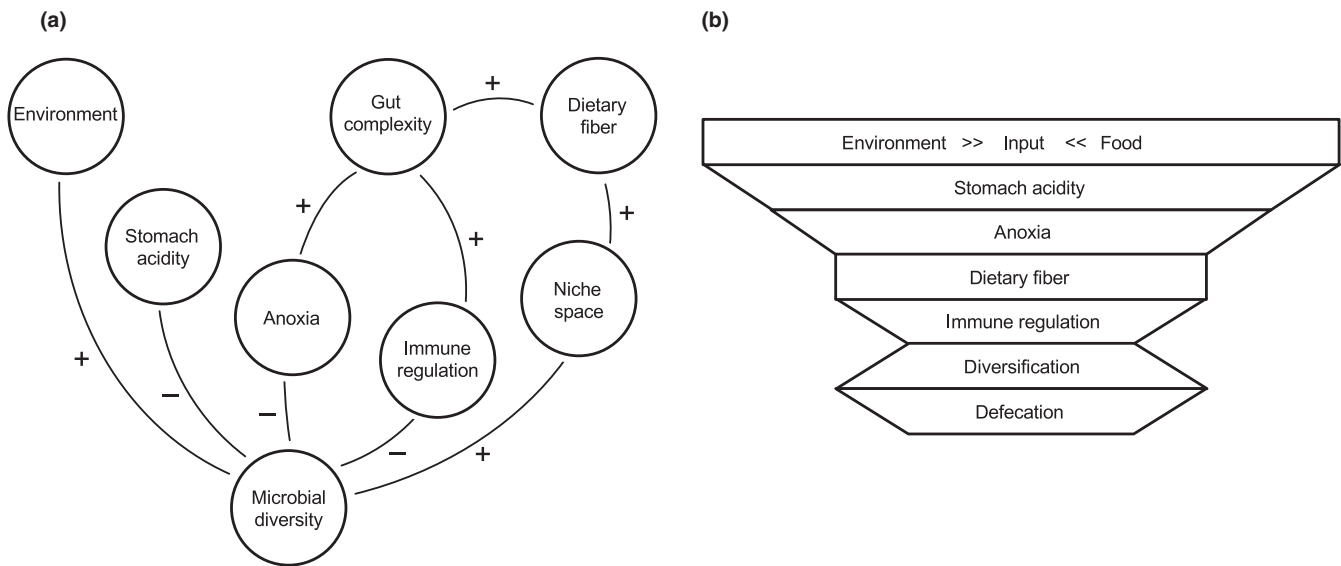


FIGURE 1 The gut embodies ecological processes that either positively or negatively impact microbial diversity. Gut features and their influences on diversity are diagrammed here as a relationship network (a) and longitudinal steps through the gut (b)

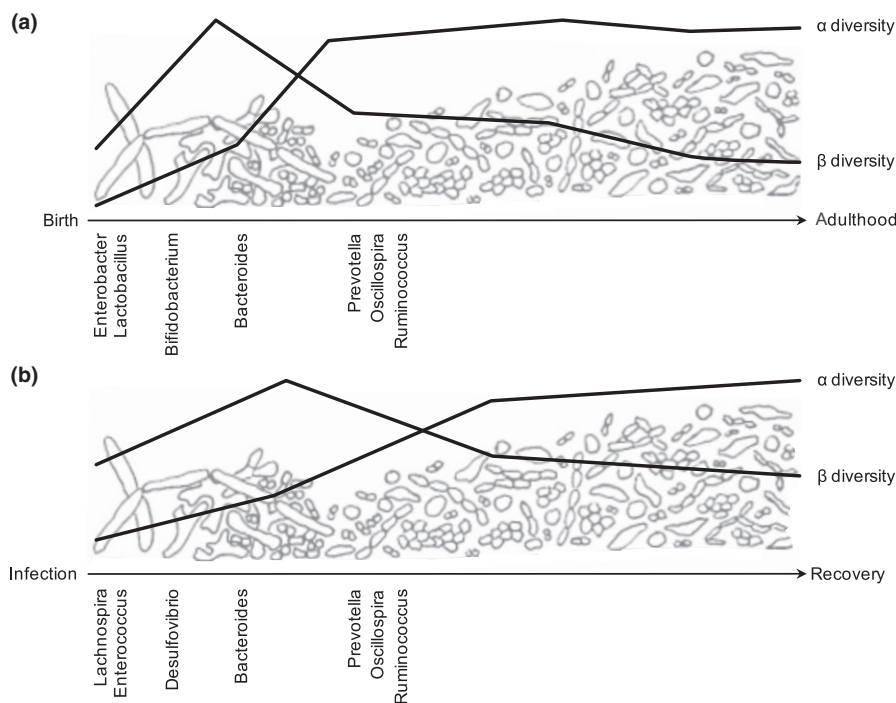


FIGURE 2 Microbiomes undergo similar colonization processes after birth and disease events. Community complexity, measured by alpha diversity, increases as opportunistic pioneer species give way to beneficial mutualists. Conversely, the variation between microbiomes, measured by beta diversity, decreases as membership converges towards the climax community typical of a healthy adult. (a) Primary succession dynamics from birth to weaning were characterized in three lemur species (Erin A McKenney et al., 2015) and correlated with metagenomic enrichment and functional specialization specific to each host species (McKenney, Greene et al., 2017; McKenney, O'Connell et al., 2017). (b) Secondary succession dynamics were characterized in folivorous lemurs infected with *Cryptosporidium* (McKenney, Greene et al., 2017; McKenney, O'Connell et al., 2017)

characterized by metagenomic enrichment and functional specialization specific to each host diet (McKenney, Greene et al., 2017; McKenney, O'Connell et al., 2017; McKenney et al., 2015). Similarly, gut microbiomes follow different trajectories to recover initial

community composition after disturbance by enteric disease (McKenney, Greene et al., 2017). In both cases, opportunistic species are common in the environment and readily colonize the gut; but these early invaders are typically out-competed in later stages

of succession (Figure 2A) (McKenney et al., 2015). While these opportunists and potential pathogens also proliferate in gut environments where diarrhoea or antibiotic treatment disrupt the stable climax community (Figure 2B) (Chang et al., 2008; McKenney, Greene et al., 2017; McKenney, O'Connell et al., 2017), they too are out-competed as subjects recover and resume consuming a high-fibre diet.

Although the four ecological processes of dispersal, environmental selection, diversification and drift are critical for determining and/or shaping microbial membership in the hindgut community, and thus apt for purposes of analogy, the effect of the gut microbiome on the host may be better conceptualized by an ecosystem service framework. Organisms and habitats collectively perform beneficial functions, referred to as ecosystem services, which contribute to ecosystem stability and production. In macroecology, ecosystem services provide a framework for conceptualizing ecosystem dynamics and interdependence. More recently, ecosystem services have been assigned monetary values to emphasize their economic importance and to inform public and private policy (Braat & de Groot, 2012; Costanza et al., 1997). Here, we outline a “microbiome services” framework, which similarly incorporates supporting services, provisioning services, regulating services and cultural services (Table 1).

3 | MICROBIOME SERVICES

3.1 | Supporting services

Supporting services, such as pioneer products, biofilm formation and nutrient cycling, make all other services possible; they are the “first

TABLE 1 Key services provided (or potentially provided) by the microbiome to the host and the ecosystem services to which they correspond. Here, it is key to bear in mind that a service can be either positive (a beneficial service) or negative, a disservice from the host perspective

Category	Ecosystem services ^a	Microbiome services
Supporting	Primary production	Pioneer products
	Soil formation	Biofilm formation
	Nutrient cycling	e.g., Methanogenesis, urea
Provisioning	Food, energy	Short chain fatty acids
	Genes, medicine	Antibiotics
	Minerals	Vitamins
	Ornaments	Scent and coloration
Regulating	Waste decomposition	Detoxification
	Pest/disease control	Colonization resistance, immunomodulation
	Climate regulation	Resilience, functional overlap
Cultural	Cognitive development	Mood, anxiety/depression
	Customs, rituals	Fermented food/drink

^aMillennium Ecosystem Assessment (2005).

step” to sustainable ecosystems, from which all other services derive. Pioneer products—the metabolites produced by initial colonizing taxa—provide a foundation for community development, in the same way that primary production supplies an energy source for food webs by converting light to carbohydrates (Millennium Ecosystem Assessment, 2005; De Groot, Wilson, & Boumans, 2002). Initial colonization inherently transforms the environment, creating niche space for additional species (McNally & Brown, 2015). For example, many pioneer species, which colonize the gut at birth and remain in the nursing infant, are oxygen tolerant (i.e., Enterobacteriaceae) (McKenney et al., 2015). These pioneer species consume oxygen and produce metabolites that alter the gut environment (i.e., by changing pH or by stimulating the development of the host immune system or intestinal tissue). Together, these pioneer products promote the growth of anaerobic species and other taxa more typical of the stable climax communities found in healthy adults (i.e., Ruminococcaceae) (McKenney et al., 2015; McNally & Brown, 2015).

Another important aspect of microbial colonization involves biofilm formation across the intestinal mucus membrane, analogous to soil formation. The cost to bacteria of the cooperation required to form a biofilm is outweighed by the potential benefits of reduced predation on large numbers of cells and the increased efficiency of interactions between those cells (Rainey & Rainey, 2003). The biofilm itself also changes the spatial and chemical features of the environment (Rainey & Travisano, 1998): each microbe's discrete physiological differences contribute to the environmental gradients and heterogeneity that ultimately increase niche diversity (Donaldson, Lee, & Mazmanian, 2016). Microbial metabolites not only feed other microbial taxa (a process referred to as “cross-feeding”), but often double as chemical signals to other microbial species and to the host (Estrela, Whiteley, & Brown, 2015). Some metabolites, such as butyrate, stimulate host intestinal cell specialization (Leser & Mølbak, 2009), while others train the host immune system to distinguish microbial mutualists and commensals from potential pathogens. In this way, environmental engineering paves the way for the microbial species typical of climax communities in healthy adults, by altering the host ecosystem to provide for and favour those climax species.

After a food web has established, the ecosystem is sustained by nutrient cycling—the process by which nutrients move from the environment (host gut and ingesta) to microbes, between microbes and the host, and ultimately back to the environment (Martiny et al., 2015). A special case of the “cross-feeding” mentioned above, nutrient cycling promotes ecosystem stability by maximizing energy harvest and increasing microbial niche space (Estrela et al., 2015). In the gut, microbes use nutrient cycling to reclaim and provide nutrients that are otherwise unavailable to the host. For example, microbial digestion of starch and fibre unlocks carbon sources for diverse bacteria as well as the host by producing short chain fatty acids (SCFA) and glucose, with hydrogen gas as a by-product (Stevens & Hume, 1998). SCFA are removed via host absorption (see further discussion of SCFA under *Provisioning services*); but archaea use the hydrogen gas as a substrate to produce methane, thereby removing that

product to further catalyse fermentation. While glucose can be converted directly to CO₂ and H₂, this global reaction does not release as much energy as the process of methanogenesis. By integrating two tiers of nutrient cycling, methanogenic microbial communities maximize energy harvest from available fermentation substrates.

The urea cycle offers another mode of nutrient cycling, in which nitrogen is passed between the host and its microbes (Martiny et al., 2015; Stevens & Hume, 1998). Bacteria in the gut first break down dietary and endogenous sources of amino acids to produce bacterial protein and ammonia. The ammonia is next transported to the liver to provide raw material for host protein synthesis. Some of the resulting urea waste product is then returned to the gut for microbial conversion to ammonia. A previous study detected significantly enriched pathways for nitrogen reclamation via the urea cycle in folivorous (leaf-eating) compared to frugivorous (fruit-eating) lemurs (McKenney, Greene et al., 2017; McKenney, O'Connell et al., 2017). In other words, animals that eat diets low in nitrogen have developed mechanisms, including partnership with microbes, to reclaim more nitrogen from their food than would otherwise be provided.

3.2 | Provisioning services

Microbial provisioning services create material benefits including SCFA, antibiotics, vitamins, coloration and scent, for the host. While fibre is inaccessible to most mammalian hosts, SCFA can be absorbed and used by the host metabolism (Stevens & Hume, 1998). Starch is fermented to produce the fatty acid propionate, which fuels gluconeogenesis, the metabolic pathway that results in glucose production (Stevens & Hume, 1998). This pathway is especially important in cattle and other animals that do not consume dietary sugar. Fermentation of fibre produces the fatty acids butyrate and acetate, which are used for ATP synthesis. Butyrate is used on-site by intestinal cells, while acetate is transported to peripheral muscle tissues to be converted to ATP or adipose (Stevens & Hume, 1998).

Microbial production of antibiotics may benefit the host, either directly by inhibiting the growth of pathogens (see colonization resistance under *Regulating services*) (Estrela et al., 2015) or indirectly by altering host metabolism to promote weight gain. Low doses of antibiotics have been used in the food industry to increase animal growth rates for decades (Feighner & Dashkevich, 1987; Quigley, Drewry, Murray, & Ivey, 1997), and increased antibiotic use and exposure correlate with increased obesity in humans (Riley, Raphael, & Faerstein, 2013).

Gut microbes also produce vitamins that satisfy host requirements and prevent oxidative stress. For example, gut microbes supplement exogenous sources of B-vitamins (i.e., folate and B₁₂) and vitamin K (Hill, 1997; LeBlanc et al., 2013), which mammalian hosts cannot produce. Other vitamins, such as A and C, are microbially synthesized from cofactors (i.e., acetyl-CoA) and carotenoids, which are exclusively synthesized by plants and microbes. Carotenoids are not only precursors to vitamin A, but also provide antioxidant protection against free-radical damage, meaning that gut microbes not only supplement vitamin requirements but may

also prevent inflammatory disease and colon cancer (Vachali, Bhosale, & Bernstein, 2012).

Carotenoids comprise some of the most ubiquitous pigments in nature and contribute to visual communication in addition to physiological health (Vachali et al., 2012). Goldfinch feathers, red-spotted newt juveniles, flamingos' pink (derived from pink shrimps, which in turn get their colour from microscopic red algae) and even the yellow-orange of duck and chicken legs, all owe their characteristic hues to carotenoids. Bacteria may also contribute to plumage colour in birds structurally, by colonizing the surface of the feathers (Shawkey, Pillai, Hill, Siefferman, & Roberts, 2007). Coloration plays a role in communication, particularly mate selection, suggesting yet again that microbes affect their host's fitness. Most social animals, however, communicate information (e.g., age, sex, physiological status) through scent, and a large part of the scent profile is attributable to skin bacteria (Kuhn & Natsch, 2009). Separate studies have documented distinct bacterial communities that appear to mediate the different chemical profiles in the scent glands of wild hyenas (Theis et al., 2013) and meerkats (Leclaire, Jacob, Greene, Dubay, & Drea, 2017).

3.3 | Regulating services

Microbiomes provide a safeguard to stabilize and maintain environmental conditions through detoxification, colonization resistance, resilience and functional overlap. Similarly, microbiomes provide regulating services that help to maintain a stable environment in and on the host. For example, gut microbiota play an important role in detoxification of "biohazardous waste" comprising poisonous or other undesirable ingesta that hosts cannot digest. Many plants produce secondary compounds to deter herbivores. These chemical defences come in many flavours (although most are bitter): some act directly as poison (i.e., creosote) (Kohl & Dearing, 2016); others prevent the absorption of nutrients and minerals (i.e., tannins, phytic acid) (McKenney, Greene et al., 2017; McKenney, O'Connell et al., 2017); and some even disrupt the reproductive cycle (i.e., phytoestrogens: If you cannot beat them, prevent future generations from being born). To varying extents, the gut microbiome can adapt to digest any ingesta that the host cannot; and this includes secondary compounds. By breaking down these compounds, gut microbes effectively detoxify otherwise harmful foods. Gut microbes facilitate intake of creosote and tannins in wood rats (Kohl & Dearing, 2016), and McKenney et al. detected enriched microbial metabolic pathways for tannin and phytic acid degradation in folivorous lemurs (McKenney, Greene et al., 2017; McKenney, O'Connell et al., 2017).

A diverse gut ecosystem can also regulate populations of pests or disease. In the gut, climax microbial communities provide colonization resistance against pathogens by competing for available resources. With all niches occupied, invasive pathogens are left with restricted access to resources and persist at low levels or not at all. Indeed, only when the healthy gut microbiome is decimated by antibiotics can *Clostridium difficile* wreak havoc on human health (Waaaij, 1989). In addition to outcompeting pathogens, commensal

microbes help the host protect itself by modulating the immune system directly (Forsythe & Bienenstock, 2010).

Stable microbial communities with high diversity not only resist colonization by pathogens (Estrela et al., 2015); they are also considered more resilient to changing conditions (Lozupone, Stombaugh, Gordon, Jansson, & Knight, 2012). High-diversity microbiomes provide a buffer to change by utilizing available resources through a combination of functional overlap and niche specialization. Different microbial species may produce similar digestive enzymes that break down the same substrate, but the performance of each species is optimized under different environmental conditions (McNally & Brown, 2015). This physiological “variation on a theme” (also discussed in reference to biofilm formation under *Supporting services*) ensures that community-level function is preserved over time.

3.4 | Cultural services

We can define microbial cultural services as ones that enrich host behavioural, social and aesthetic experience. Indeed, shifts in (or absence of) gut microbiota have been shown to impact neural development in vertebrates, cognitive function, mood and behaviour (Luna & Foster, 2015). For example, microbes influence our social interactions via scent and visual signals (see *Provisioning services*). They also directly impact our cognitive development and day-to-day function (Sampson & Mazmanian, 2015): Atypical gut community composition has been tied to tantrums in toddlers (Christian et al., 2015) and anxiety and depression—or avoidance thereof—in adults (Marin et al., 2017). Direct modulations are probably achieved through the production of neuroactive molecules including neurotransmitters, hormones and SCFA, which are readily absorbed into the bloodstream and often small enough to cross the blood–brain barrier (Dinan, Stilling, Stanton, & Cryan, 2015). Gut microbes may be especially important to primates and other social animals, as they contribute to individual recognition and social interactions (Archie & Tung, 2015). Thus, social interactions and group size may both facilitate and be mediated by transmission of microbiota (Montiel-Castro, González-Cervantes, Bravo-Ruiseco, & Pacheco-López, 2013).

Beyond the body, microbial cultures lie at the heart of human cultures. Thousands of varieties of fermented foods and drinks play key social and nutritional roles in human societies (Katz, 2016; Steinkraus, 1997), including bread (Gobbetti, Minervini, Pontonio, Di Cagno, & De Angelis, 2016), beer, wine, cheese, yoghurt, sauerkraut and kimchee (Jung et al., 2011). Several of the microbial taxa found in fermented foods (i.e., *Lactobacillus*, *Enterococcus*, *Streptococcus*, *Actinobacteria*, *Klebsiella* and *Pseudomonas*) (Tamang, Watanabe, & Holzapfel, 2016) are also associated with the human body (Huttenhower et al., 2012). These shared taxa also perform similar functions to the gut microbiome, digesting food substrates to produce vitamins and SCFAs. The latter products, particularly lactic acid and acetic acid, decrease pH, thereby altering the environment to select against potential pathogens and further promote growth of beneficial fermentative populations (Tamang, Shin, Jung, & Chae, 2016). Together, the functional roles of microbes in fermented foods often involve

improvement in flavours, nutritional qualities and storage abilities. Fermented foods thus not only provide an additional exogenous source of microbial supplements, but also serve to enrich and distinguish the diversity of human cultures.

4 | DISCUSSION

4.1 | Predicting host fitness

Microbes are increasingly credited with driving functional characteristics that are classically considered to be host-derived (i.e., behaviours and scent, as described above). Assuming that microbiome services increase the fitness of the host, the absence of such services should negatively impact host fitness. Our microbiome services perspective thus helps to explain overarching patterns and inform hypothesis development. Below, we outline specific cases when we would expect more microbes to fit a particular process.

We first predict that provisioning and regulating services increase fitness in animals that consume high-fibre or toxic foods. Mammals are dependent on their gut microbes to digest dietary fibre. Therefore, herbivores tend to evolve complex gut morphologies characterized by elongated intestines and/or a voluminous caecum (Chivers & Hladik, 1984; Stevens & Hume, 1998), both to facilitate the growth of fermentative communities and to maximize provisioning services (i.e., fermentative productivity). In addition to containing dietary fibre, some plants also produce secondary defence compounds that either prevent nutrient absorption (i.e., tannins) or are toxic to herbivores (i.e., creosote). In animals that consume these toxic plants, the gut microbiota provides regulating services (i.e., detoxification). This functional role has been established in wood rats (Kohl & Dearing, 2016), but we predict that detoxification probably also benefits folivorous lemurs (McKenney, Greene et al., 2017; McKenzie, O'Connell et al., 2017) and other herbivores. Furthermore, additional detoxification pathways (i.e., metal metabolism) may offer protection to animals in disturbed or polluted habitats, thus enhancing their likelihood for survival in inhospitable environments and, consequently, their reproductive fitness.

Next, we propose that provisioning services may have increased value to the host in specific habitats. While several factors including historical biogeography, resource availability and predation are known to influence the distribution of herbivores, gut microbial fermentation also facilitates the host niche through metabolite provisioning (Amato et al., 2015). Fermentation produces heat as well as metabolites (Dale, Stewart, & Brody, 1954), and consequently, the heat of fermentation may potentially benefit the hosts, particularly for animals that live in cold climates. In such cases, microbes may even be credited with facilitating the ability of herbivores to live at high altitudes by conferring an indirect thermoregulatory advantage to their hosts.

Finally, we predict that animals at high risk of infection by pathogens will benefit from regulating services, specifically colonization resistance (Lozupone et al., 2012). Previous studies have linked “immature” or disrupted microbial communities with susceptibility to infection, with younger animals exhibiting more acute symptoms and

greater GM variation. A study of captive lemurs infected with *Cryptosporidium* (McKenney, Greene et al., 2017; McKenzie, O'Connell et al., 2017) validates this prediction by demonstrating that mature animals are far more robust to infection than are juveniles. This finding reinforces the idea that fully developed GMs may be more resilient to enteric disease. Indeed, decreased GM diversity is associated with *Clostridium difficile* infection in human adults (Chang et al., 2008), and whole faecal community transplants provide the most effective, reliable method to treat antibiotic-resistant *C. difficile* infection (Petrof et al., 2013), further suggesting that colonization resistance prevents pathogenicity.

Conversely, the same microbial functions that we predict would benefit a host might become disadvantageous outside of the co-evolutionary context. One example of mismatch is (de)toxification and hemochromatosis. Tannins bind iron, but if the gut microbiome breaks down tannins in an animal adapted to a low-iron diet, that species may develop iron storage disease. This phenomenon has been documented in several captive mammalian species (Clauss, Lechner-Doll, Hänichen, & Hatt, 2002), including black rhinoceros (Mylniczenko, Sullivan, Corcoran, Fleming, & Valdes, 2012).

4.2 | Maximizing the benefits of microbiome services

Given the diverse set of services that microbial communities provide to their hosts, it is perhaps not surprising that practices are common among animals to facilitate the establishment of these communities. For example, many mammals practise coprophagy—the deliberate ingestion of one's own or a conspecific's faeces—which is known to maximize benefits from gut microbes (Hirakawa, 2001; Hume, 1989). After birth, infant horses and folivorous lemurs (*P. coquereli*) ingest their dams' faeces to seed their gut with the beneficial microbes they will need to digest their high-fibre diets in adulthood. In early life stages, coprophagy may indirectly increase host fitness by seeding the gut with a diverse, beneficial microbial community (Montiel-Castro et al., 2013). Bulk inoculation during infancy is especially beneficial to herbivores, which depend on gut microbes to digest plant material (Stevens & Hume, 1998). However, many hindgut fermenters also regularly ingest their own or family members' faeces throughout adulthood, as a nutritional supplement. Consumption of faeces by hindgut fermenters "reclaims" microbial fermentation products (i.e., SCFA and vitamins) that are produced in the caecum and colon but may not be completely absorbed before defecation. This behaviour has been extensively documented in rabbits (Hirakawa, 2001), but would presumably also benefit other hindgut fermenters. Coprophagy has been documented in wild lemurs (Fish, Sauther, Loudon, & Cuozzo, 2007; Loudon & Sauther, 2013), gorillas (Graczyk & Cranfield, 2003) and bonobos (Sakamaki, 2010), as well as captive chimpanzees (Hopper, Freeman, & Ross, 2016). Microbiome services thus offer a framework to better understand whether and when the host ecosystem might be in need of conservation.

We have discussed several examples of microbiome services, but it is important to remember that the host-microbiome system is one that is dynamic and in constant flux. Host and microbe are engaged

in an arms race, and each would like to cheat the other (i.e., maximize the service of their competitor while minimizing cost). While services in general can be evaluated using a variety of measures, the chosen metrics are critical for clarifying the relationship between hosts and their microbes. For example, host reproductive fitness or metrics of health can be measured to gauge the relative impact or value of services such as microbial metabolites, which can also be quantified. Future efforts to quantify and compare the net effects of microbiome services across multiple hosts and contexts (i.e., health status, life stage and environment) will therefore be critical to advancing our understanding of the host-microbiome relationship.

DATA ACCESSIBILITY

The data used to produce Figure 2 are publicly available in the NCBI Sequence Read Archive, Project Numbers PRJNA270617 and PRJNA376003, respectively.

AUTHOR CONTRIBUTION

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REFERENCES

- Amato, K. R., Leigh, S. R., Kent, A., Mackie, R. I., Yeoman, C. J., Stumpf, R. M., ... Garber, P. A. (2015). The gut microbiota appears to compensate for seasonal diet variation in the wild black howler monkey (*Alouatta pigra*). *Microbial Ecology*, *69*(2), 434–443. <https://doi.org/10.1007/s00248-014-0554-7>
- Archie, E. A., & Tung, J. (2015). Social behavior and the microbiome. *Current Opinion in Behavioral Sciences*, *6*, 28–34. <https://doi.org/10.1016/j.cobeha.2015.07.008>
- Beasley, D. E., Koltz, A. M., Lambert, J. E., Fierer, N., & Dunn, R. R. (2015). The evolution of stomach acidity and its relevance to the human microbiome. *PLoS One*, *10*(7), e0134116. <https://doi.org/10.1371/journal.pone.0134116>
- Bodelier, P. L. (2011). Toward understanding, managing, and protecting microbial ecosystems. *Frontiers in Microbiology*, *2*, 1–8.
- Braat, L. C., & de Groot, R. (2012). The ecosystem services agenda: Bridging the worlds of natural science and economics, conservation and development, and public and private policy. *Ecosystem Services*, *1*(1), 4–15. <https://doi.org/10.1016/j.ecoser.2012.07.011>
- Chang, J. Y., Antonopoulos, D. A., Kalra, A., Tonelli, A., Khalife, W. T., Schmidt, T. M., & Young, V. B. (2008). Decreased diversity of the fecal microbiome in recurrent *Clostridium difficile*—associated diarrhea. *The Journal of Infectious Diseases*, *197*(3), 435–438. <https://doi.org/10.1086/525047>
- Chivers, D. J., & Hladik, C. M. (1984). Diet and gut morphology in primates. In D. J. Chivers, B. A. Wood & A. Bilsborough (Eds.), *Food acquisition and processing in primates* (pp. 213–230). Berlin, Germany: Springer. <https://doi.org/10.1007/978-1-4757-5244-1>
- Cho, I., & Blaser, M. J. (2012). The human microbiome: At the interface of health and disease. *Nature Reviews Genetics*, *13*(4), 260–270. <https://doi.org/10.1038/nrg3182>

- Christian, L. M., Galley, J. D., Hade, E. M., Schoppe-Sullivan, S., Dush, C. K., & Bailey, M. T. (2015). Gut microbiome composition is associated with temperament during early childhood. *Brain, Behavior, and Immunity*, 45, 118–127. <https://doi.org/10.1016/j.bbi.2014.10.018>
- Clauss, M., Lechner-Doll, M., Hänichen, T., & Hatt, J. (2002). Excessive iron storage in captive mammalian herbivores—a hypothesis for its evolutionary etiopathology. *Proceedings of the European Association of Zoo and Wildlife Veterinarians*, 4, 123–131.
- Costanza, R., d'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., ... Paruelo, J. (1997). The value of the world's ecosystem services and natural capital. *Nature*, 387(6630), 253. <https://doi.org/10.1038/387253a0>
- Costello, E. K., Stagaman, K., Dethlefsen, L., Bohannan, B. J., & Relman, D. A. (2012). The application of ecological theory toward an understanding of the human microbiome. *Science*, 336(6086), 1255–1262. <https://doi.org/10.1126/science.1224203>
- Dale, H., Stewart, R., & Brody, S. (1954). Rumen temperature. 1. Temperature gradients during feeding and fasting. *Cornell Veterinarian*, 44, 368–374.
- De Groot, R. S., Wilson, M. A., & Boumans, R. M. (2002). A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics*, 41(3), 393–408. [https://doi.org/10.1016/S0921-8009\(02\)00089-7](https://doi.org/10.1016/S0921-8009(02)00089-7)
- Dinan, T. G., Stilling, R. M., Stanton, C., & Cryan, J. F. (2015). Collective unconscious: How gut microbes shape human behavior. *Journal of Psychiatric Research*, 63, 1–9. <https://doi.org/10.1016/j.jpsychires.2015.02.021>
- Donaldson, G. P., Lee, S. M., & Mazmanian, S. K. (2016). Gut biogeography of the bacterial microbiota. *Nature Reviews Microbiology*, 14(1), 20–32. <https://doi.org/10.1038/nrmicro3552>
- Estrela, S., Whiteley, M., & Brown, S. P. (2015). The demographic determinants of human microbiome health. *Trends in Microbiology*, 23(3), 134–141. <https://doi.org/10.1016/j.tim.2014.11.005>
- Feighner, S. D., & Dashkevich, M. P. (1987). Subtherapeutic levels of antibiotics in poultry feeds and their effects on weight gain, feed efficiency, and bacterial cholytaurine hydrolase activity. *Applied and Environmental Microbiology*, 53(2), 331–336.
- Fierer, N., Ferrenberg, S., Flores, G. E., González, A., Kueneman, J., Legg, T., ... O'Neill, S. P. (2012). From animalcules to an ecosystem: Application of ecological concepts to the human microbiome. *Annual Review of Ecology, Evolution, and Systematics*, 43, 137–155. <https://doi.org/10.1146/annurev-ecolsys-110411-160307>
- Fish, K. D., Sauther, M. L., Loudon, J. E., & Cuzzo, F. P. (2007). Coprophagy by wild ring-tailed lemurs (*Lemur catta*) in human-disturbed locations adjacent to the Beza Mahafaly Special Reserve, Madagascar. *American Journal of Primatology*, 69(6), 713–718. [https://doi.org/10.1002/\(ISSN\)1098-2345](https://doi.org/10.1002/(ISSN)1098-2345)
- Forsythe, P., & Bienenstock, J. (2010). Immunomodulation by commensal and probiotic bacteria. *Immunological Investigations*, 39(4–5), 429–448. <https://doi.org/10.3109/08820131003667978>
- Foster, K. R., Schluter, J., Coyte, K. Z., & Rakoff-Nahoum, S. (2017). The evolution of the host microbiome as an ecosystem on a leash. *Nature*, 548(7665), 43. <https://doi.org/10.1038/nature23292>
- Gobbetti, M., Minervini, F., Pontonio, E., Di Cagno, R., & De Angelis, M. (2016). Drivers for the establishment and composition of the sourdough lactic acid bacteria biota. *International Journal of Food Microbiology*, 239, 3–18. <https://doi.org/10.1016/j.ijfoodmicro.2016.05.022>
- Graczyk, T. K., & Cranfield, M. R. (2003). Coprophagy and intestinal parasites: Implications to human-habituated mountain gorillas (*Gorilla gorilla beringei*) of the Virunga Mountains and Bwindi Impenetrable Forest. *Primate Conservation*, 19(58), 4.
- Hill, M. (1997). Intestinal flora and endogenous vitamin synthesis. *European Journal of Cancer Prevention*, 6(2), S43–S45. <https://doi.org/10.1097/00008469-199703001-00009>
- Hirakawa, H. (2001). Coprophagy in leporids and other mammalian herbivores. *Mammal Review*, 31(1), 61–80. <https://doi.org/10.1046/j.1365-2907.2001.00079.x>
- Hopper, L. M., Freeman, H. D., Ross, S. R. (2016). Reconsidering coprophagy as an indicator of negative welfare for captive chimpanzees. *Applied Animal Behaviour Science*, 176, 112–119.
- Hume, I. (1989). Optimal digestive strategies in mammalian herbivores. *Physiological Zoology*, 62(6), 1145–1163. <https://doi.org/10.1086/physzool.62.6.30156206>
- Huttenhower, C., Gevers, D., Knight, R., Abubucker, S., Badger, J. H., Chinwalla, A. T., ... Fulton, R. S. (2012). Structure, function and diversity of the healthy human microbiome. *Nature*, 486(7402), 207. <https://doi.org/10.1038/nature11234>
- Jung, J. Y., Lee, S. H., Kim, J. M., Park, M. S., Bae, J.-W., Hahn, Y., ... Jeon, C. O. (2011). Metagenomic analysis of kimchi, a traditional Korean fermented food. *Applied and Environmental Microbiology*, 77(7), 2264–2274. <https://doi.org/10.1128/AEM.02157-10>
- Katz, S. E. (2016). *Wild fermentation: The flavor, nutrition, and craft of live-culture foods*. Hartford, VT: Chelsea Green Publishing.
- Kohl, K. D., & Dearing, M. D. (2016). The woodrat gut microbiota as an experimental system for understanding microbial metabolism of dietary toxins. *Frontiers in Microbiology*, 7, 1–9.
- Koskella, B., Hall, L. J., & Metcalf, C. J. E. (2017). The microbiome beyond the horizon of ecological and evolutionary theory. *Nature Ecology & Evolution*, 1(11), 1606. <https://doi.org/10.1038/s41559-017-0340-2>
- Kuhn, F., & Natsch, A. (2009). Body odour of monozygotic human twins: A common pattern of odorant carboxylic acids released by a bacterial aminoacylase from axilla secretions contributing to an inherited body odour type. *Journal of the Royal Society Interface*, 6(33), 377–392. <https://doi.org/10.1098/rsif.2008.0223>
- LeBlanc, J. G., Milani, C., de Giori, G. S., Sesma, F., Van Sinderen, D., & Ventura, M. (2013). Bacteria as vitamin suppliers to their host: A gut microbiota perspective. *Current Opinion in Biotechnology*, 24(2), 160–168. <https://doi.org/10.1016/j.copbio.2012.08.005>
- Leclaire, S., Jacob, S., Greene, L. K., Dubay, G. R., & Drea, C. M. (2017). Social odours covary with bacterial community in the anal secretions of wild meerkats. *Scientific Reports*, 7, 3240. <https://doi.org/10.1038/s41598-017-03356-x>
- Lemanceau, P., Maron, P.-A., Mazurier, S., Mougel, C., Pivato, B., Plassart, P., ... Wipf, D. (2015). Understanding and managing soil biodiversity: A major challenge in agroecology. *Agronomy for Sustainable Development*, 35(1), 67–81. <https://doi.org/10.1007/s13593-014-0247-0>
- Leser, T. D., & Mølbak, L. (2009). Better living through microbial action: The benefits of the mammalian gastrointestinal microbiota on the host. *Environmental Microbiology*, 11(9), 2194–2206. <https://doi.org/10.1111/j.1462-2920.2009.01941.x>
- Ley, R. E., Peterson, D. A., & Gordon, J. I. (2006). Ecological and evolutionary forces shaping microbial diversity in the human intestine. *Cell*, 124(4), 837–848. <https://doi.org/10.1016/j.cell.2006.02.017>
- Loudon, J. E., & Sauther, M. L. (2013). Verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed lemur (*Lemur catta*) endoparasitism at the Beza Mahafaly Special Reserve. *Madagascar Conservation & Development*, 8(1), 21–28.
- Lozupone, C. A., Stombaugh, J. I., Gordon, J. I., Jansson, J. K., & Knight, R. (2012). Diversity, stability and resilience of the human gut microbiota. *Nature*, 489(7415), 220–230. <https://doi.org/10.1038/nature11550>
- Luna, R. A., & Foster, J. A. (2015). Gut brain axis: Diet microbiota interactions and implications for modulation of anxiety and depression. *Current Opinion in Biotechnology*, 32, 35–41. <https://doi.org/10.1016/j.copbio.2014.10.007>
- Marin, I. A., Goertz, J. E., Ren, T., Rich, S. S., Onengut-Gumuscu, S., Farber, E., ... Gaultier, A. (2017). Microbiota alteration is associated with the development of stress-induced despair behavior. *Scientific Reports*, 7, 43859. <https://doi.org/10.1038/srep43859>

- Martiny, J. B., Jones, S. E., Lennon, J. T., & Martiny, A. C. (2015). Microbiomes in light of traits: A phylogenetic perspective. *Science*, 350(6261), aac9323. <https://doi.org/10.1126/science.aac9323>
- McFall-Ngai, M., Hadfield, M. G., Bosch, T. C., Carey, H. V., Domazet-Lošo, T., Douglas, A. E., ... Gilbert, S. F. (2013). Animals in a bacterial world, a new imperative for the life sciences. *Proceedings of the National Academy of Sciences of the United States of America*, 110(9), 3229–3236. <https://doi.org/10.1073/pnas.1218525110>
- McKenney, E. A., Greene, L. K., Drea, C. M., & Yoder, A. D. (2017). Down for the count: Cryptosporidium infection depletes the gut microbiome in Coquerel's sifakas. *Microbial Ecology in Health and Disease*, 28(1), 1335165. <https://doi.org/10.1080/16512235.2017.1335165>
- McKenney, E. A., O'Connell, T. M., Rodrigo, A., & Yoder, A. D. (2017). Feeding strategy shapes gut metagenomic enrichment and functional specialization in captive lemurs. *Gut Microbes*. <https://doi.org/10.1080/19490976.2017.1408762>
- McKenney, E. A., Rodrigo, A., & Yoder, A. D. (2015). Patterns of gut bacterial colonization in three primate species. *PLoS One*, 10(5), e0124618. <https://doi.org/10.1371/journal.pone.0124618>
- McNally, L., & Brown, S. P. (2015). Building the microbiome in health and disease: Niche construction and social conflict in bacteria. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 370(1675), 20140298. <https://doi.org/10.1098/rstb.2014.0298>
- Millennium Ecosystem Assessment (2005). *Ecosystems and human well-being: Synthesis*. In J. Sarukhan & A. Whyte Eds., pp. v–vii). Washington, DC: Island Press.
- Montiel-Castro, A. J., González-Cervantes, R. M., Bravo-Ruiseco, G., & Pacheco-López, G. (2013). The microbiota-gut-brain axis: Neurobehavioral correlates, health and sociality. *Frontiers in Integrative Neuroscience*, 7, 1–16.
- Mylniczenko, N. D., Sullivan, K. E., Corcoran, M. E., Fleming, G. J., & Valdes, E. V. (2012). Management strategies of iron accumulation in a captive population of black rhinoceroses (*Diceros bicornis minor*). *Journal of Zoo and Wildlife Medicine*, 43(3s), S83–S91. <https://doi.org/10.1638/2011-0168.1>
- Nemergut, D. R., Schmidt, S. K., Fukami, T., O'Neill, S. P., Bilinski, T. M., Stanish, L. F., ... Wickey, P. (2013). Patterns and processes of microbial community assembly. *Microbiology and Molecular Biology Reviews*, 77(3), 342–356. <https://doi.org/10.1128/MMBR.00051-12>
- Petrof, E. O., Gloor, G. B., Vanner, S. J., Weese, S. J., Carter, D., Daigneault, M. C., ... Allen-Vercove, E. (2013). Stool substitute transplant therapy for the eradication of *Clostridium difficile* infection: 'RePOOPulating' the gut. *Microbiome*, 1(1), 3. <https://doi.org/10.1186/2049-2618-1-3>
- Quigley, J., Drewry, J., Murray, L. M., & Ivey, S. (1997). Body weight gain, feed efficiency, and fecal scores of dairy calves in response to galactosyl-lactose or antibiotics in milk replacers. *Journal of Dairy Science*, 80(8), 1751–1754. [https://doi.org/10.3168/jds.S0022-0302\(97\)76108-3](https://doi.org/10.3168/jds.S0022-0302(97)76108-3)
- Rainey, P. B., & Rainey, K. (2003). Evolution of cooperation and conflict in experimental bacterial populations. *Nature*, 425(6953), 72. <https://doi.org/10.1038/nature01906>
- Rainey, P. B., & Travisano, M. (1998). Adaptive radiation in a heterogeneous environment. *Nature*, 394(6688), 69. <https://doi.org/10.1038/27900>
- Relman, D. A. (2012). The human microbiome: Ecosystem resilience and health. *Nutrition Reviews*, 70(s1), s2–s9.
- Riley, L. W., Raphael, E., & Faerstein, E. (2013). Obesity in the United States—dysbiosis from exposure to low-dose antibiotics? *Frontiers in Public Health*, 1, 1–8.
- Sakamaki, T. (2010). Coprophagy in wild bonobos (*Pan paniscus*) at Wamba in the Democratic Republic of the Congo: A possibly adaptive strategy? *Primates*, 51(1), 87. <https://doi.org/10.1007/s10329-009-0167-9>
- Sampson, T. R., & Mazmanian, S. K. (2015). Control of brain development, function, and behavior by the microbiome. *Cell Host & Microbe*, 17(5), 565–576. <https://doi.org/10.1016/j.chom.2015.04.011>
- Shawkey, M. D., Pillai, S. R., Hill, G. E., Siefferman, L. M., & Roberts, S. R. (2007). Bacteria as an agent for change in structural plumage color: Correlational and experimental evidence. *The American Naturalist*, 169(S1), S112–S121. <https://doi.org/10.1086/510100>
- Steinkraus, K. H. (1997). Classification of fermented foods: Worldwide review of household fermentation techniques. *Food Control*, 8(5–6), 311–317. [https://doi.org/10.1016/S0956-7135\(97\)00050-9](https://doi.org/10.1016/S0956-7135(97)00050-9)
- Stevens, C. E., & Hume, I. D. (1998). Contributions of microbes in vertebrate gastrointestinal tract to production and conservation of nutrients. *Physiological Reviews*, 78(2), 393–427. <https://doi.org/10.1152/physrev.1998.78.2.393>
- Stilling, R. M., Bordenstein, S. R., Dinan, T. G., & Cryan, J. F. (2014). Friends with social benefits: Host-microbe interactions as a driver of brain evolution and development? *Frontiers in Cellular and Infection Microbiology*, 4, 147.
- Tamang, J. P., Shin, D.-H., Jung, S.-J., & Chae, S.-W. (2016). Functional properties of microorganisms in fermented foods. *Frontiers in Microbiology*, 7, 1–13.
- Tamang, J., Watanabe, K., & Holzapfel, W. (2016). Review: Diversity of microorganisms in global fermented foods and beverages. *Frontiers in Microbiology*, 7, 377.
- Theis, K. R., Venkataraman, A., Dycus, J. A., Koonter, K. D., Schmitt-Matzen, E. N., Wagner, A. P., ... Schmidt, T. M. (2013). Symbiotic bacteria appear to mediate hyena social odors. *Proceedings of the National Academy of Sciences of the United States of America*, 110(49), 19832–19837. <https://doi.org/10.1073/pnas.1306477110>
- Toft, C., & Andersson, S. G. (2010). Evolutionary microbial genomics: Insights into bacterial host adaptation. *Nature Reviews Genetics*, 11(7), 465–475. <https://doi.org/10.1038/nrg2798>
- Vachali, P., Bhosale, P., & Bernstein, P. S. (2012). Microbial carotenoids. In J.-L. Barredo (Ed.), *Microbial carotenoids from fungi: Methods and protocols* (pp. 41–59). Totowa, NJ: Humana Press. <https://doi.org/10.1007/978-1-61779-918-1>
- Vellend, M. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, 85(2), 183–206. <https://doi.org/10.1086/652373>
- Waaij, V. (1989). The ecology of the human intestine and its consequences for overgrowth by pathogens such as *Clostridium difficile*. *Annual Reviews in Microbiology*, 43(1), 69–87. <https://doi.org/10.1146/annurev.mi.43.100189.000441>
- Walter, J., & Ley, R. (2011). The human gut microbiome: Ecology and recent evolutionary changes. *Annual Review of Microbiology*, 65, 411–429. <https://doi.org/10.1146/annurev-micro-090110-102830>

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