Trends in
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Feature Review

The island biology of the host microbiome

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Microbiomes perform critical functions for their hosts, and understanding microbiome variation is important for both basic and applied science. However, host traits alone cannot explain the entirety of microbiome variation, because, alongside host traits, microbiomes are shaped by multiple ecological processes. Researchers have thus turned to theories of island biology, conceptualising animal hosts as islands and animal microbiomes as metacommunities that assemble within and disperse between host islands. To develop realistic models, this host-as-island metaphor must be examined by explicitly comparing geological and host islands. Here, we critically examine the host-as-island metaphor by evaluating how microbiome variation is shaped by the four metacommunity processes that explain biodiversity on geological islands: local interspecies interactions, local selection, dispersal, and stochasticity. Key differences between host islands and geological islands include the complexity of microbiome transmission networks arising from host mobility and sociality and the capacity of hosts to evolve to control their microbiomes. We conclude with discussions of how eco-evolutionary dynamics differ between geological islands and host islands, and the reciprocal relevance of island biology and microbiome science.

Highlights

The extraordinary biodiversity of the host-associated gut microbiome cannot be explained exclusively by host traits.

Researchers have interpreted hosts as biological islands suitable for microbial colonisation and have applied ecological theories of island biogeography and metacommunity ecology to further understand microbiome composition and variation.

To benefit from the host-as-island metaphor, the metacommunity processes characterising macroscopic and microbial diversity should be explicitly compared. On geological islands, these processes include interspecies interactions, local selection, interisland dispersal, and ecological stochasticity. In host islands, these processes are paralleled by interactions between microbes, host selection, microbial transmission, and microbial stochasticity, respectively.

A critical difference between host islands and geological islands is that host islands are mobile and undergo adaptive evolution, whereas geological islands do not.

Microbiome variation, metacommunity ecology, and the host-as-island metaphor

Animal microbiomes—the microbial communities and their collective genes and gene products characterising animal hosts—display extraordinary biodiversity. Microbiomes play crucial roles in host physiology (e.g., metabolism [1], immunity [2], hormones [3], and the nervous system [4]), effects that can, in turn, influence host behaviour [5]. Overall, the microbiome has broad consequences for animal ecology and evolution [6–8].

As a target of significant biomedical interest, the microbiome was understandably initially approached from a largely biomedical perspective that prioritised host traits (e.g., genes, physiology, diet, and behaviour [1,9–12]) as key drivers of microbiome variation. However, host trait variation explains only a small fraction of microbiome variation. For instance, analyses of hundreds of host traits across thousands of participants accounted for no more than ~15% of total taxonomic variation in the human gut microbiome [9,12].

The limited power of host traits to explain microbiome variation is at least partly rooted in the fact that broader ecological circumstances constrain microbiome variation on which host-mediated selection can operate. This by no means suggests that host traits are unimportant in accounting for the microbiome's taxonomic variation (indeed, they are extremely important). However, it is also necessary to elucidate the other factors that govern and contribute to the composition of an individual microbiome. For instance, **host control** (see Glossary) over intrinsic microbial populations is contingent on microbial acquisition: hosts cannot impose selection on microbial taxa before they reach the host. Whilst microbial acquisition is indeed partially under host control, microbial acquisition is an inherently stochastic process, with chance or random exposures

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exerting significant effects [13]. For obligate anaerobes, transmission between hosts requires surviving the oxygen-rich external environment, lower temperature, and gastric acid, making successful interhost dispersal relatively rare and episodic. In this sense, a host in many ways resembles a habitable island whose **community assembly** is constrained by vast, uninhabitable seas. Thus, to understand host microbiome variation, we must consider influences on microbiomes beyond those exerted by host traits.

The microbiome is usefully conceptualised as an ecological system nested within a physiological system (the host), which is, in turn, nested within larger-scale social and ecological systems. Thus, in addition to the effects of individual host physiology on the microbiome, a significant proportion of microbiome variation arises from processes occurring at other ecological scales: between microbes within the host and between hosts [14]. Notably, these ecological processes operate under varying degrees of host control and experience some degree of stochasticity (see Figure 1, Key figure).

The integration of ecological theories and physiological processes has contributed substantially to our understanding of the microbiome and host–microbiome interactions [14–23]. This includes, for instance, explanations of phenomena such as **microbiome community assembly** across host ontogeny [24] and the context-dependent pathogenesis of microbes such as *Escherichia coli* [25,26]. One promising approach has been the application of theories of island biology—namely **island biogeography** [27,28] and its intellectual descendant, **metacommunity ecology** [29,30]—to discern patterns of microbiome variation within and between hosts [14,15,19,21] (Box 1). As ecological communities, animal microbiomes inhabit a **fragmented landscape**, with microbes spreading between habitable patches (hosts), akin to the ecology of macroscopic communities inhabiting and dispersing across islands or islandlike ecosystems (e.g., mountaintops, glades, copses, tree-crowns, glades, groves, and lakes). The island metaphor is certainly not a new one in ecology and evolutionary biology: Daniel Janzen previously referred to individual plants as islands for insects [36], and William Freeland referred to primate social groups as biological islands for intestinal parasites [37]. The application of the island metaphor to host microbiomes can be considered an extension of these earlier uses [15,21]. However, understanding the gut microbiome in terms of island biology is an important exercise in its own right, owing both to the growing interest in the microbiome and the emergence of new ecological tools, methods, and concepts. For instance, similar to geological islands, the compositional divergence of the gut microbiome tends to increase with geographic distance between host individuals [38,39] and species [40]. Furthermore, the **species–area relationship** (the ecological principle that more diverse species communities are found on larger geological islands [41,42]) operates at the microbial level. This holds both for free-living microbial metacommunities such as water-filled tree hole microbiomes [43], as well as host-associated microbiomes where more diverse communities tend to occur on larger host islands [44–46].

Despite the apparent metaphorical utility and expedience of the host-as-island metaphor, host microbiomes also differ from geological islands in crucial respects. For instance, animal hosts interact with one another to produce connectivity patterns between microbiomes that are far more complex than those occurring in dispersal between geological islands. Furthermore, host islands undergo adaptive evolution to manipulate their microbiomes [47,48], resulting in local selection patterns and feedback-loops vastly more intricate than those occurring on geological islands.

Here, we critically evaluate the metaphor of the host–microbiome system as an **island ecosystem** to explain microbiome variation. Analysing a metaphor is typically a literary exercise and not

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Key figure

Metacommunity processes characterising variation on geological islands and host islands

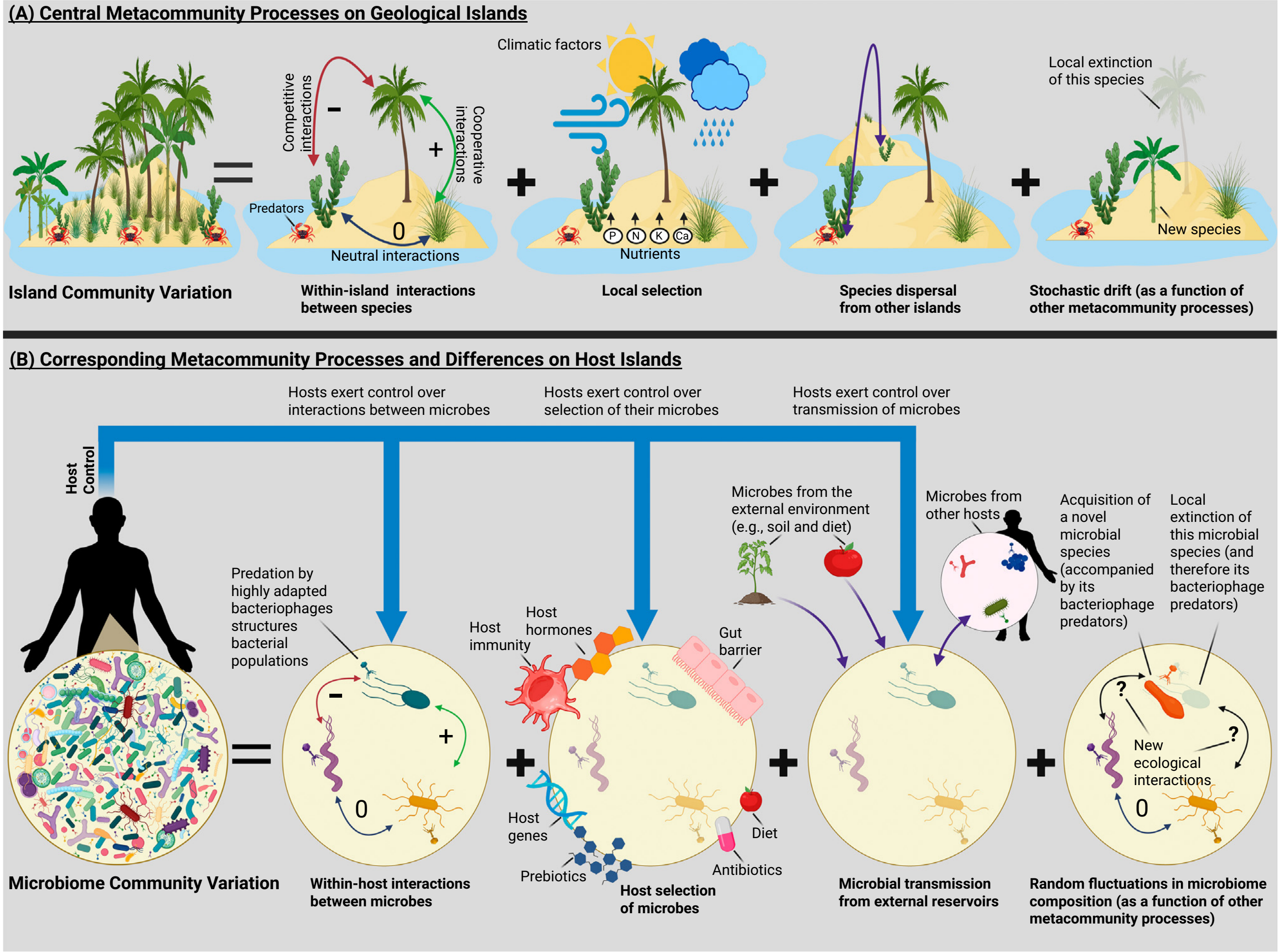

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Figure 1. (A) The total biodiversity on a geological island can be explained as a function of four metacommunity processes: intraisland interactions occurring between species (including negative, neutral, and positive interactions), local selection entailing forces that affect species survival (including climatic factors and nutrient availability), the dispersal of species from neighbouring islands, and stochastic effects that occur as a function of the other three processes, with some species suffering extinction or others arriving at random. (B) In parallel to ecological community variation on geological islands, microbiome variation on host islands can also be explained in terms of these four metacommunity processes. Thus, microbiome variation is a function of the interactions between members of the microbiome (which may be negative, neutral, or positive, and which include the presence of predators such as bacteriophages), host selection (the top-down physiological influence that the host exerts over its microbiome), transmission of microbes from external reservoirs (other hosts or the general environment), and stochastic events in which some microbes go extinct or others arrive at random. Alongside broad similarities, there are also critical differences in how these processes operate on geological and host islands. In particular, host islands are mobile and undergo adaptive evolution, which are not relevant processes for geological islands. Moreover, host islands exert control over their microbes via manipulating three of these metacommunity processes (ecological interactions, selection, and transmission). Such top-down control does not occur on geological islands. Both the similarities and differences must be accounted for to fully appreciate and exploit the value of the host-as-island metaphor. This figure was created using BioRender.com.

one in which scientists routinely engage, especially nowadays [49]. However, as fundamental cognitive tools for interpreting the world [49,50], metaphors themselves can exert profound but hidden consequences on our perceptions and the formation of knowledge [49,51]. All metaphors

Box 1. Island biogeography and metacommunity ecology

Island biology is a broad term that we use to cover multiple theories of the ecology of fragmented landscapes, including island biogeography, metapopulation ecology, and metacommunity ecology. In this review, we focus on island biogeography and its contemporary formalisation, metacommunity ecology. Island biogeography is the leading explanatory framework for the ecology of spatially distinct islands [27,28,31], as well as islandlike systems [32] (e.g., lakes, mountaintops, forests separated by grasslands, and oases). Island biogeography theory has focused on predicting the diversity of species on islands as a function of the island's area and distance from source populations (e.g., the mainland or other islands). Two central and strongly supported predictions of the theory are that (i) ***α*-diversity** (i.e., diversity of species on a given island) is lower on smaller and more remote islands that experience higher rates of extinction versus colonisation and (ii) that ***β*-diversity** (i.e., dissimilarity of island species communities) is higher amongst more spatially distant islands [31].

The theory of metacommunity ecology was developed to analyse how multispecies communities assemble on islandlike systems [30], combining the principles of island biogeography with traditional community ecology [33] and metapopulation ecology [34]. Metacommunity ecology focuses on how ecological communities on islands arise simultaneously as a function of local processes operating within island boundaries (e.g., species' ecological niches, local environmental conditions, and competition for resources) and regional processes operating across the entire metacommunity of interconnected islands (e.g., dispersal of species between islands). The species composition of an archipelago ecosystem arises as a function of four metacommunity parameters [35]: (i) ecological interactions amongst species within an island (within-island species interactions), (ii) selective filtering of species due to varying abiotic island characteristics (local selection), (iii) movement of species between islands (dispersal), and (iv) **stochastic drift**. Simulation models have demonstrated how the diversity and stability of ecological communities depend on the combination of all four of these metacommunity parameters [35].

are imperfect, and thus examining the metaphor generates discussion, which can, in turn, reveal concealed biases or assumptions. In other words, a literary exercise may bear scientific fruit [49].

We undertake this literary task in this review by explicitly comparing ecological processes on geological islands and host islands, identifying key similarities, differences, and uncertainties. We suggest ways to update models of island biology to better capture the ecological reality of host-associated microbiomes. We focus on the four central processes of metacommunity ecology that shape community composition on geological islands: local biotic interactions, local abiotic selection, dispersal, and stochasticity (Figure 1A). We examine these against analogous processes shaping the composition of gut microbiomes (i.e., host islands): microbe–microbe interactions within the microbiome, within-host selection, microbial transmission, and stochasticity in microbiome composition (Figure 1B).

Researchers have already discussed the importance of some of these metacommunity processes for understanding microbiome variation [14,15]. In this review, we synthesise all four processes. We then discuss the value of **network analysis** in understanding transmission in microbial metacommunities nested within host social networks (a critical difference between geological islands and host islands). We also compare eco-evolutionary dynamics across geological and host islands. Finally, we discuss the reciprocal relevance of island biology and microbiome science. Our emphasis throughout will be on the animal gut microbiome, but this approach is applicable, in principle, to microbiomes at all body sites (Box 2).

Comparing metacommunity ecology in geological islands and host islands

In this review, we compare how macroscopic communities inhabiting geological islands and microbial communities inhabiting host islands are shaped by four central metacommunity processes: (i) species interactions, (ii) local selection, (iii) transmission, and (iv) stochasticity (Figure 1).

Species interactions on geological islands and host islands

Microbes inhabiting host islands do not operate in isolation from one another. Rather, like macroscopic organisms inhabiting geological islands, microbial species inhabiting host islands engage in various ecological interactions with one another in microbiome communities, which exert

Glossary

***α*-diversity:** Species richness and evenness at a site (e.g., species richness or Shannon evenness in a gut microbiome).

***β*-diversity:** Pairwise dissimilarities in species presence and abundance between sites (e.g., dissimilarities in the gut microbiomes across a social network).

***γ*-diversity:** Total species pool across multiple related sites (e.g., all bacterial species in an environment, including those inhabiting various host body sites, or all bacterial species observed within a host population).

Alternative stable equilibria: Descriptions of ecological systems that can stably operate or exist in multiple in different states. These states are maintained by intrinsic forces, despite otherwise similar or identical external conditions.

Bacterial warfare: Bacteria have evolved numerous strategies for attacking and defending against competing bacterial lineages. These strategies entail both physical and chemical processes, and include various secretion system types, antibiotics, and even local suicide.

Biotic resistance: The phenomenon in which macroscopic species resident in an ecological community inhibit the spread of foreign or novel species.

Colonisation resistance: Intrinsic microbes prevent pathogen invasion and establishment via outcompeting the pathogens by effective use of shared ecological resources, modifying the local environment, or directly occupying space the invaders would have exploited. Colonisation resistance is a central benefit that commensal and mutualistic microbes provide to hosts.

Community assembly: The ecological processes via which a community (a group comprising members of multiple interacting species) is formed.

Cross-feeding: A process in which different bacterial species consume one another's metabolic byproducts.

Direct social transmission: Interhost microbial transmission mediated by direct (physical) social interactions between hosts, including licking, suckling, copulation, grooming, and all other forms of physical contact between hosts. Direct social transmission may also occur through very intimate non-physical social interactions, such as close proximity.

Box 2. Hosts as biological archipelagos

There are multiple distinct (though related) ways in which we can apply the island metaphor to study the microbiome. In this review, we have employed a very specific interpretation: we treat each host as a single island, and within this interpretation, we have focused mainly on the gut microbiome. By extension, a group or network of hosts can be considered a biological archipelago of gut microbiomes [21]. This interpretation treats each host as a more-or-less homogeneous island. However, a geological island is far from homogeneous and can itself comprise multiple ecosystems (e.g., beaches, forests, lakes, and mountains). Thus, an island can also be considered an archipelago in terms of the different habitats it provides for different species. In the same way, any host can itself be viewed as an archipelago comprising multiple islands with different ecosystems. This is because each host body site harbours a unique microbiome. For instance, the human body comprises multiple microbiomes, including gut, skin, oral, vaginal, lung, and nasal microbiomes [52]. On average, these communities are distinct from one another, separated by physical and physiological barriers, as well as the capacities of the microbes themselves. We would not, for example, expect anaerobic gut microbes to thrive amongst aerotolerant skin microbes. However, some degree of microbial dispersal could occur between islands within the host (e.g., mouth→gut transmission, or across sites in the gastrointestinal tract [53]). Whilst in some cases such intrahost, between-island transmission may be typical or tolerated, in others, it may indicate pathology [54].

There is also much work on anatomical and physiological segmentation in the gut and microbial distributions within the gut [55], making each individual gut an archipelago rather than an island. The same is true for the oral microbiome (i.e., different microbiomes associated with the tongue, teeth, gums, and so on [56]—each of which can be considered as distinct islands for microbes). In these cases, we would expect high rates of transmission between islands owing to close proximity amongst the islands (though it does not follow that dispersing microbes will survive in the new habitats). Thus, each host comprises multiple archipelagos.

We do not consider these alternative perspectives in this review, but it is nonetheless worth pointing out that the island metaphor can be applied at several levels, and each may yield biological and health-relevant insights.

significant effects on community composition [16] (Figure 1). Moreover, hosts exert some degree of control over the ecological interactions between their microbes—a phenomenon we discuss in greater detail in Box 3.

Ecological interactions occur on both geological islands and host islands. Several ecological interactions within microbiomes on host islands are readily comparable to those occurring in macroscopic communities on geological islands. The interactions may be neutral, antagonistic

Box 3. Host control over within-microbiome ecological interactions between microbes

A key difference between geological islands and host islands is that host islands undergo adaptive evolution to shape their microbiomes for their own benefit. These processes are broadly captured under the phenomenon of host control [48]. Whilst much host control occurs via the evolution of physiological mechanisms that directly limit or facilitate the growth of particular microbes (processes of host selection), host control of the microbiome also entails mechanisms involving other metacommunity processes (Figure 1), including host control of microbe–microbe interactions.

Hosts can regulate within-microbiome ecological interactions in several ways. For instance, hosts may house specific beneficial microbes in dedicated organs or tissues to limit the competition these microbes would otherwise face in more open and diverse environments. In this vein, the beewolf cultivates *Streptomyces* bacteria in special antennal glands [57], the bobtail squid houses *Aliivibrio fischeri* bacteria in its light-organ [58], and mammals may generate spatial structure in their gut microbiomes via colonic crypts [59]. These spatial constraints allow hosts to adaptively harbour microbial populations by allowing the coexistence of otherwise competitive taxa in spatially distinct anatomical regions. On the other hand, hosts can also actively increase the likelihood that different microbial taxa will come into proximity and compete within the gut via mechanisms such as peristalsis and segmentation that homogenise gut microbial populations.

There is also evidence that hosts directly manipulate cell–cell signaling between bacteria in the microbiome, a process that can regulate competition between microbes. For instance, mammals produce a mimic of the widely used **quorum sensing** molecule autoinducer-2, with consequences for interbacterial communication and competition, including biofilm formation, cell division, and motility [60]. Similarly, the cnidarian *Hydra* modifies the quorum sensing signal of its *Curvibacter* symbiont, enhancing its proliferation [61]. Finally, hosts can also promote interactions between microbial taxa within the gut by regulating the production of mucus that provides an attachment point to enhance phage predation of bacteria [62]. Overall, therefore, hosts are capable of exerting significant control over the microbe–microbe interactions in the gut environment [48].

Ecological guild: Groups of species in a community that exploit the same ecological resources (or that exploit distinct resources in the same way).

Ecological network: The set of interactions occurring amongst members (taxa) of an ecological community (e.g., predation, parasitism, cooperation).

Ecological succession: The phenomenon of predictable community composition change over time.

Ecosystem engineer: A species that exerts substantial effects on the local environment (e.g., habitat destruction or significant modification of the physical structure or chemical composition of the environment).

Enterosignature: A classification of interindividual microbiome variation as a relative combination of bacterial signatures, generalising specific axes of community variation. For example, the human gut microbiome is proposed to have five general enterosignatures dominated by *Bacteroides*, Bacillota (Firmicutes), *Prevotella*, *Bifidobacterium*, and *Escherichia*. Each individual hosts a microbiome with a dynamic combination of these signatures.

Environmental transmission: A form of microbial transmission that entails the acquisition and addition of external microbes (e.g., from soil or the diet) to the host's intrinsic microbiome.

Founder effects: The phenomenon in which a new population formed by a smaller subset of a larger source population displays lower genetic diversity (i.e., genetic bottleneck) than the source population.

Fragmented landscape: A landscape in which various habitats are patchy and separated (e.g., islands separated by water) rather than contiguous.

Horizontal gene transfer: A process in which a bacterium acquires the genetic material of another bacterium (e.g., plasmids) and incorporates it into its own genome. This enhances genomic diversity and confers novel biosynthetic and metabolic capabilities in the receiving bacterium (e.g., antibiotic resistance genes emerging in one bacterium can enhance antibiotic resistance in another community member via horizontal gene transfer).

Host control: The processes by which a host controls its intrinsic microbial populations to exploit microbial physiological and ecological processes for its own benefit whilst limiting microbially-mediated harm. Host control (e.g., competitive exclusion of similar-niche taxa from the same system [63] and outright **bacterial warfare** [64]), or cooperative (e.g., **cross-feeding** [65]). All of these relationships occur, for instance, between various members of the prominent human gut bacterial genus *Bacteroides* [66,67].

However, rather less is known about how the roles of the various other ecological interactions differ between geological islands and host islands. For example, compared to macroscopic communities on geological islands where trophic relationships exert strong influences on community composition, the extent to which predator–prey interactions amongst microbes influence microbiomes remains unclear. There are certainly some salient examples of predator–prey relationships in the microbiome: for instance, bacteriophages (viruses that 'hunt' bacteria) can exert strong effects on gut microbiome structure and function [68]. Similarly, ciliates are now recognised as voracious predators of bacteria in gut ecosystems, though their ecological significance beyond the rumen is poorly understood [69]. Furthermore, the abundance and diversity of predatory bacteria (such as those in the genus *Bdellovibrio*) in animal microbiomes are associated with higher microbiome diversity [70]. This pattern is consistent with the diversifying effects of coexisting with predators on many geological islands [71]. Despite such evidence, it is not known whether these predator–prey relationships form true trophic chains, or whether they influence microbiomes inhabiting host islands to the same extent as on geological islands.

Competitive interactions exert stronger effects on host islands than geological islands. Compared to macroscopic communities inhabiting geological islands, gut microbiomes inhabiting host islands seem to be enriched in competitive interactions, with mutualistic interactions between microbes being rare [16]. This might be because bacteria live in extremely dense environments that lack prominent trophic structure, as previously discussed. Some microbes do indeed consume the metabolic byproducts of others [65] (i.e., cross-feeding). However, many others compete for the same host-provided nutrients (digesta and host secretions [48]) rather than generating nutrients via autotrophic processes. At least some others hunt one another in the manner of macroscopic organisms inhabiting geological islands.

The extent to which ecological interactions in a host microbiome are competitive (compared to cooperative) influences the microbiome as a whole [24]. For instance, cooperative interactions increase community productivity because cross-feeding effectively exploits all available resources [72]. At the same time, competitive microbial interactions can increase community stability [16]. This is because competitive relationships can limit the domino-type cascading collapses that are common in ecosystems characterised by high degrees of interdependence or cooperation amongst organisms. High degrees of cooperation can render a system susceptible to cheaters and free riders [16]. Indeed, cooperative interactions have long been theorised to destabilise animal and plant communities in macroscopic ecosystems [73], although this does not universally occur [74]. Importantly, recent research has suggested that the stabilising effect of competition is perhaps more unambiguous in microbial communities on host islands than macroscopic ones on geological islands [16]. One explanation for this phenomenon may be that, owing to the reduced trophic structure in microbial communities, competition is the main defence against **invasion** [15] (a destabilising event in which one species expands disproportionately at the expense of others). In microbiome systems, invasions affect both other community members and host health [22]. This is comparable in some ways to invasions on geological islands. In both cases, a successful invasion depends not only on the competitive capacities of the invader (e.g., the virulence of the pathogen) but also on the susceptibility of the resident community to invasion (e.g., available niche space). For instance, the phenomenon of **biotic resistance** in plant communities is based on evidence that more species-rich plant communities tend to be more resilient to invasions [75,76]. In this vein, it was recently demonstrated that the diversity of the

mechanisms include processes of host selection of microbes via the host's physiology (e.g., selective filtering of microbes by immune system) and behaviour (e.g., choosing specific dietary substrates). Host control mechanisms also include manipulating the ecological interactions between microbes and the transmission of other microbes.

Host feeding: The phenomenon in which the host selectively provisions its intrinsic microbes with nutrients.

Indirect social transmission: Interhost microbial transmission mediated by the environment rather than direct social interaction (e.g., one host acquires microbes shed into the environment by another host sharing the environment, without direct physical contact between hosts).

Island biogeography: A theory that describes and predicts species distributions on islands.

Island ecosystem: An ecosystem characterised by habitable patches separated by an inhospitable interpatch matrix and connected by limited species dispersal between patches. Islands in archipelagoes separated by water are the canonical examples of such ecosystems. Other examples include mountaintop sky islands, lakes, and disjunct forested habitats.

Invasion: The arrival and proliferation of a non-native species in an ecosystem to which it is not otherwise endemic, with potentially significant ecological changes and consequences.

Jump-diffusion processes: Stochastic process where changes that would typically occur continuously and gradually instead progress through sudden, unpredictable "jumps".

Metacommunity ecology: A theory of species distributions in a set of fragmented ecological communities (each comprising multiple interacting species) connected to one another via the dispersal of residents. The composition of each community in a metacommunity is shaped by within-community interactions between species, within-community local selection, between-community dispersal of species, and stochastic fluctuations.

Microbiome community assembly: The ecological processes by which a microbiome is formed.

Multilayer network: A network comprising multiple layers describing different types of interactions or murine gut microbiome linearly increased the capacity to resist pathogen invasion because more diverse sets of resident bacteria saturated the available niche space and outcompeted the invader (i.e., **colonisation resistance**) [26]. Indeed, colonisation resistance is one of the attributes of microbiome ecology with the greatest relevance for host health, and hosts may adaptively modify the competitive networks of their microbiomes to enhance colonisation resistance.

Ecological networks shape communities on both geological islands and host islands. The ecological interactions amongst species in a community form an **ecological network**. Microbial interactions are, of course, difficult to observe directly. Instead, they are commonly inferred from their covariation across space and time or via coculturing experiments (Box 4). Because all species comprising a community are connected to one another via these ecological networks, ecological communities can undergo internally driven change. Paralleling processes on geological islands, microbiomes inhabiting host islands can experience internally driven ecological shifts, including **ecological succession** guided by **founder effects** [15] and shifts between **alternative stable equilibria** [15,89]. On geological islands, these internally driven dynamics can, together with local selective differences, result in community 'types' or sets of species that tend to coexist stably (e.g., forest types and lake types). In the microbiome, such variation has been described using the **enterosignature** concept, which entails continuous, ecologically driven microbiome community variation [90]. Similarly, researchers have also extended the concept of the **ecological guild** to microbial interactions [91]. To this end, two competing ecological guilds have recently been shown to characterise human microbiomes: one that metabolises fibre and is involved in **short-chain fatty acid** production, and one that is characterised by **pathobiont** presence and antibiotic resistance [92]. Overall, therefore, ecological networks play critical roles in shaping the communities of both geological islands and host islands.

Local selection on geological islands and host selection on host islands

Both macroscopic communities inhabiting geological islands and microbial communities inhabiting host islands experience selective forces from their local environments (Figure 1). On geological islands, animal and plant communities are shaped by abiotic selective forces such as climatic conditions, soil chemistry, and nutrient availability. On host islands, gut microbial communities are shaped by selective factors such as ambient pH, oxygen restriction, available nutrients, and immune activity [48]. One extremely important selection pressure imposed by mammalian hosts on their gut microbiomes is the lack of availability of oxygen, which forces

Box 4. Inferring microbial ecological networks on host islands and geological islands

Because ecological interactions within the microbiome are difficult to observe, they are often analysed using co-occurrence networks. The central idea underlying this approach is that species with overlapping niches (i.e., species competing for the same limited resources) may not inhabit the same communities [77,78]. The human skin microbiome furnishes a simple example: competitive strains of *Cutibacterium acnes* each inhabit isolated skin pores. Co-occurrence has been used as a proxy for ecological interactions in macroscopic communities as well. For instance, the so-called checkerboard patterns in species distributions observed on geological islands [79–82] have been suggested to arise from competing pairs of species inhabiting the same islands less frequently than predicted from their environmental preferences alone. On the scale of multispecies communities, these types of co-occurrence patterns have been shown to be broadly similar in both microbial and macroscopic systems [83]. However, the underlying phenomena that these patterns actually reflect are debatable. Co-occurrence patterns between species can arise not only from ecological interactions but also, and perhaps to a larger extent, from similar or different preferences for particular environments [77,78]. For instance, two species that have very different ecological niches (and are thus unlikely to compete) may occur in different kinds of communities, resulting in negative co-occurrence that is not indicative of competition.

More robust evidence for ecological interactions in microbiomes has been derived from the analysis of temporal covariance [24,84]. Coculturing experiments, in which the growth of microbial taxa is measured in isolation and in pairs [85–87], also provide robust evidence for ecological interactions occurring in microbiomes. Networks based on pairwise cocultures have revealed ecological landscapes in the gut microbiome dominated by competitive interactions [88].

associations between the same set of nodes.

Network analysis: The scientific study of complex systems via the analysis of the connections between components of those systems.

Pathobiont: A microbe that is ordinarily commensal but can become pathogenic for the host under specific conditions, such as reduced competition from other bacteria or other ecological changes. *Clostridioides difficile* is a prominent example. Under typical conditions it is harmless because it is held to low densities by competition from other gut microbes. However, it can proliferate and become pathogenic when its microbial competitors are killed (e.g., by antibiotics).

Priority effects: The effects that early-arriving species exert on a novel environment, which collectively shape emergent community structure and function. For example, early-arriving species can alter the environment to make it more favourable for themselves or less favourable for future competitors.

Short-chain fatty acid: A fatty acid comprising between two and six carbon atoms that exerts a broad range of effects on host tissue, affecting metabolic, immune, endocrine, and neural processes. The three principal SCFAs – acetate, butyrate, propionate – are produced exclusively by bacterial metabolism.

Species-area relationship: The empirical observation of a positive association between the physical area of an island and the biodiversity of its ecological communities.

Species sink: An ecosystem with sub-optimal habitat but in which biodiversity persists due to immigration from other communities.

Species source: An ecosystem with sufficient resources to permit increasing biodiversity, generating populations and communities sufficiently large to migrate to species sinks.

Social microbiome: The microbial metacommunity of an animal social network (including the microbes, their genes, and their metabolic products).

Social transmission: The process of transmitting microbes between interacting hosts.

Stepping-stone model: A description of island colonisation in which larger islands are indirectly connected to one another via smaller "stepping stone" islands that facilitate species movement between the larger islands.

microbes to ferment nutrients and synthesise products that the host can absorb [48,93,94]. Moreover, the host's diet and the digestive system exert enormous influence on the structure and function of the gut microbiome [1], effects that have been shown to outweigh those of host genetics [95]. Importantly, the host's diet and the features of its digestive system can also be considered instances of host selection, and thus a form of host control [48].

Host islands evolve to control their microbiomes, but geological islands do not. A central difference between host islands and geological islands is that host islands evolve to manipulate their microbiomes for their own benefit. In this regard, each host can be considered an **ecosystem engineer** [47,48], and each host-associated microbiome can be conceptualised as an 'ecosystem on a leash' under host control [47,48]. As discussed previously, many of these control mechanisms act via host physiological processes imposing selection on microbiomes. These mechanisms range from immune filtering of pathogenic microbes [96,97] to favouring the growth of beneficial microbes via specific nutrient provisioning (**host feeding**) [98,99]. These mechanisms jointly define which microbes can thrive on the host island. In one of the clearest examples of adaptive host selection, the bobtail squid selects for a single bacterial species, *Aliivibrio fischeri*, and exploits this bacterium's bioluminescence, it is thought, as an antipredator strategy [58]. These kinds of host-induced selective pressures diverge substantially from conventional local selection on geological islands. For instance, immune cells act more like local animal predators than abiotic selective pressures (such as temperature), and yet immune cells cannot disperse between host islands in the manner of animal predators. Overall, these control mechanisms enable the host to maintain a stable microbiome or change it in an adaptive manner to foster the host's ecological adaptation [48,100–103]. On the other hand, when shifts in the microbiome occur in the absence of host control (e.g., due to impaired immunity), they can be detrimental to host health [104]. The matter of needing to control or select colonisers in service of one's genetic fitness is, of course, irrelevant for geological islands.

On both geological and host islands, the inhabitants engage in bidirectional associations with their environments. On geological islands, several abiotic properties influencing local selection pressures (e.g., shade, soil chemistry, and nutrients) are in turn readily influenced by the macroscopic inhabitants of the island. Similarly, host selection processes that regulate the microbiome are themselves influenced by the microbiome. For example, in mice, hormonal stress responses influence the gut microbiome through changes in gut pH and motility [105]. At the same time, the gut microbiome can also regulate hormonal stress responses through specific neuronal circuits [106]. Because both hosts and their microbes evolve in response to one another, feedback mechanisms between these partners are likely stronger than those between geological islands and their inhabitants. However, the host–microbiome association is certainly not a partnership of equals: whilst hosts undergo adaptive evolution to control their microbiomes as a whole, microbiomes consist of competing taxa with conflicting genetic interests and, as such, lack the evolutionary integrity to evolve jointly to manipulate their hosts [107]. More likely, hosts are influenced by their microbiomes because they themselves have evolved to use their microbiomes as sources of ecosystem services [47].

Host selection changes with host age, resembling processes on geological islands. Young host islands in many ways resemble newly emerged volcanic islands (e.g., the Hawaiian Archipelago) or islands that rise from the depths due to lowering water levels (e.g., Baltic Sea islands). Like ecosystems on young geological islands [108], early-life microbiomes may initially be strongly shaped by transmission and stochastic processes [109]. As the host develops (e.g., immune maturation), microbiomes experience increased host selection [109,110]. This rising influence of local selection, together with the emergent local ecological network, results in predictable ecological

Stochastic drift: The phenomenon in which species arrive, establish, or suffer extinction in an ecosystem due to random events.

Quorum sensing: The phenomenon via which bacteria sense the presence and density of other bacteria, enabling cooperative and coordinated gene expression amongst bacterial members.

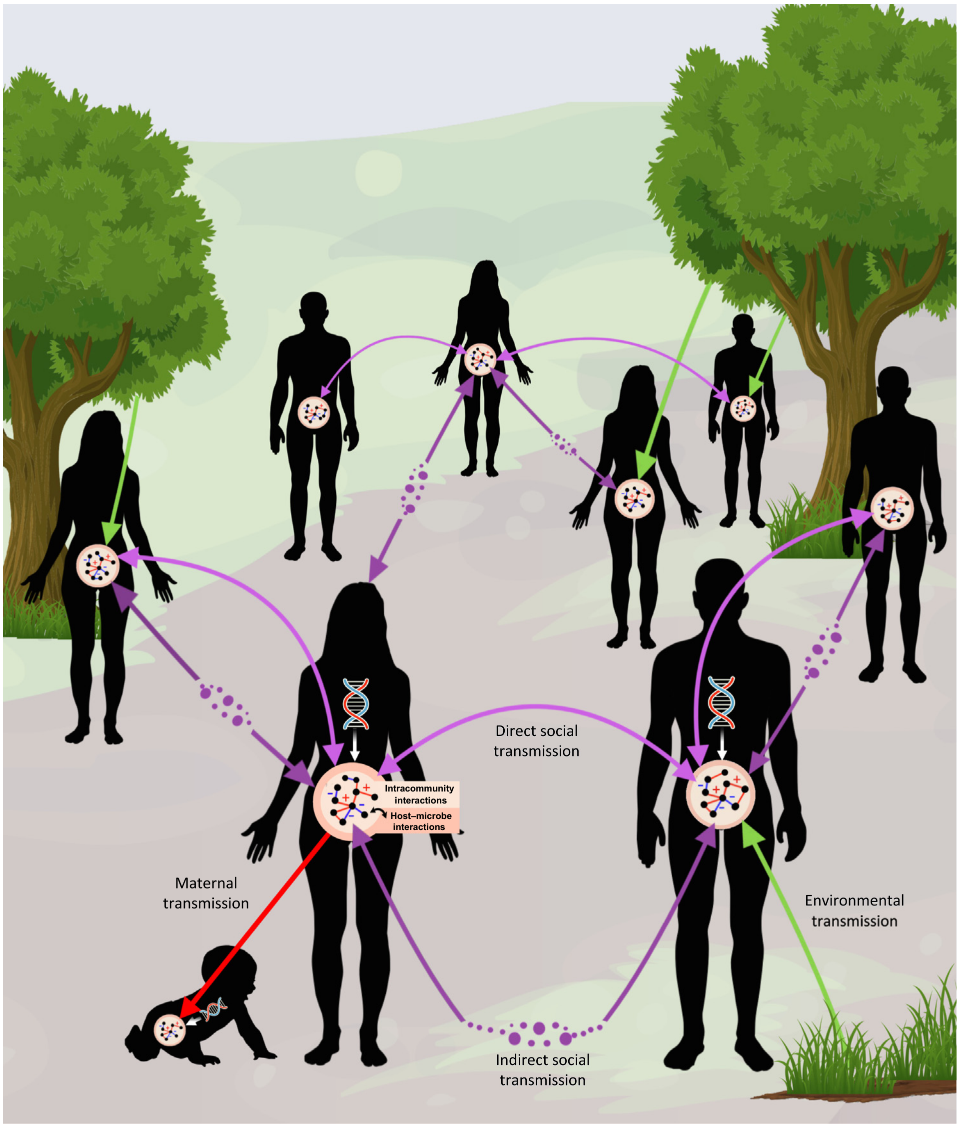
succession of the microbiome [24,111], much the same way that young macroscopic communities experience ecological succession (e.g., succession of forest communities after fires [112]). Unlike geological islands, however, the influence of host selection can also diminish (and the influence of stochastic processes can increase) as the host senesces and control mechanisms weaken (e.g., immunosenescence) [113].

Geological islands and host islands possess different generational structure. Both geological and host islands have lifespans: they emerge, persist (and change in size), and eventually disappear over time. Where geological and host islands differ, however, is that host islands reproduce, which means that new islands tend to both resemble their parental islands in their selective environments and often acquire their initial microbial communities from environments shared with their parents and relatives [22]. These two processes result in some degree of microbiome heritability [114]. **Priority effects** can aid heritability, such that the microbes establishing colonies early in the lifetime of a host are then more likely to persist or influence subsequent microbiome composition. Further, because intrahost selective systems (e.g., immune function) also possess a heritable component, microbes spreading to juvenile hosts from closely related individuals tend to face an environment at least somewhat similar to the ones to which they were adapting in the previous generation. This makes it possible for microbes to adapt to an evolving host lineage, even in the absence of specific vertical inheritance of microbes from parents to offspring.

Dispersal between geological islands and microbial transmission between host islands

A signature feature of all models of island biology is the dispersal of organisms between islands [27,28,31]. Apart from evolution, dispersal is the fundamental source of local species diversity and exerts an enormous impact on ecological communities. On geological islands, species distributions are often well-predicted by neutral models that treat ecological communities as passive products of how species spread over space [115,116]. Similarly, a critical process shaping the microbiome entails the transmission of microbes from external reservoirs [22,117]. For instance, gut microbes can be acquired via **direct social transmission**, **indirect social transmission** [22,38,39,118–122], and **environmental transmission** (e.g., from microbes in the soil [123] or the diet [124]) (Figure 2). In this regard, the host-as-island metaphor has also been particularly helpful in the **social microbiome** concept [21,22], a framework that uses island biogeography theory to consider individual hosts as biological islands and host social networks as biological archipelagos, with microbes migrating between host islands (Figure 3). Just as more diverse communities are found on more connected geological islands [125], gut microbiome diversity accumulates in more socially connected individuals compared to less socially connected individuals [39,126]. These transmission processes introduce new microbial taxa into a microbiome, though perhaps the effect of these migrations on local microbial abundances may be smaller than the effect of dispersal on species abundances across geological islands (Box 5). Overall, two of the key differences between the transmission landscapes of microbiomes and geological islands are related to the mobility and social behaviour of hosts (which we discuss below). In Box 6, we discuss two further key differences between geological islands and host islands relevant to dispersal, namely that the sea between host islands is rife with potential microbiome colonisers, and the ecological reality that species inhabiting geological islands disperse between more similar islands than microbes inhabiting host islands. In Box 7, we discuss how the phenomenon of host control extends to microbial transmission and acquisition.

Host islands are mobile, but geological islands are not. Host islands are mobile and can freely traverse the environment, influencing their exposure to microbial reservoirs. Theories of island biology assume islands are stationary, and thus the community on each island depends on species' capacities for dispersal and the geographic distance between islands [27,28]. In the



Trends in Microbiology

Figure 2. Modes of microbial transmission. Under the sterile womb hypothesis, all human (and mammalian) microbes are acquired via transmission from the external environment. We partition sources of microbial transmission into three broad categories: (i) Social microbial transmission refers to microbial transmission and acquisition from other hosts. It includes direct social transmission (in which microbes are exchanged via social interactions between hosts, shown here by solid pink arrows connecting hosts) and indirect social transmission (in which hosts shed microbes into the environment, which are then transmitted to other hosts without the need for social interaction amongst hosts, shown here by purple arrows that are broken into dots between hosts). (ii) Maternal transmission refers to the microbes that infants acquire from their mothers upon birth. These maternal microbes form the initial populations in the infant gut (and other body sites). Whilst maternal transmission is a form of social transmission, it is sufficiently important to deserve separate analysis. (iii) Environmental transmission entails the transmission of microbes from the general environment, such as the diet and the external environment (represented here with the green arrows from the trees and grass to the humans). Also shown are various host selection processes, such as host genetics, that influence microbiome variation. Within each gut microbiome, the microbes themselves engage in various ecological interactions with one another (e.g., cooperation and competition).

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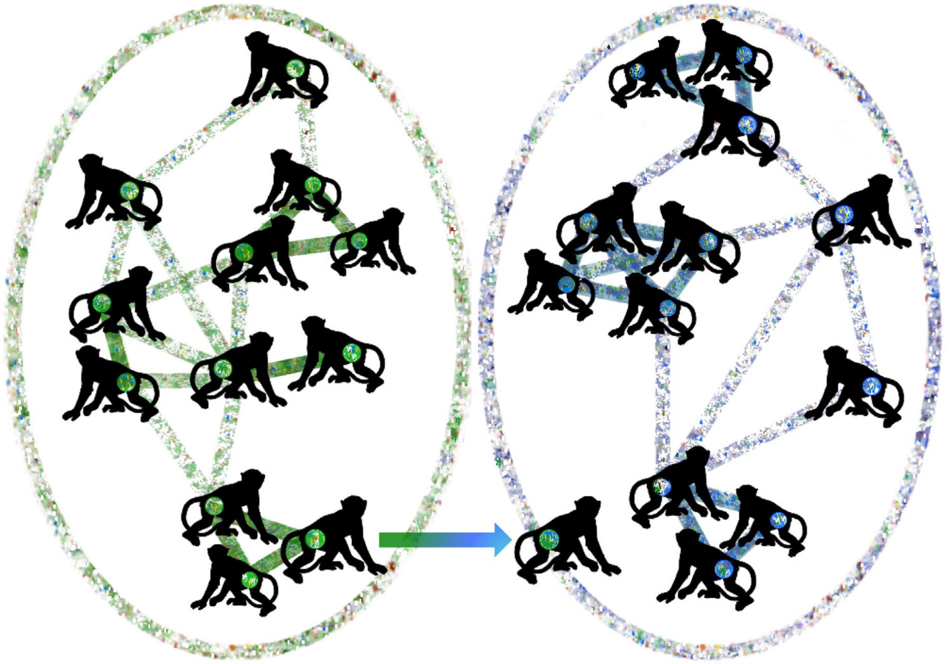

Figure 3. The social microbiome. Primate social groups (green and blue ovals) can be distinguished on the basis of microbial composition. Each monkey is a biological island for its microbes, and each social group is a biological archipelago (i.e., the social microbiome). Within each group, the degree of shading in each individual's microbiome is a function of the host's position in the social network, which determines the number and nature of social interactions. The degree of shading for edges connecting individuals represents the amount of social interaction. Hosts with more and stronger social connections harbour richer microbiomes that more closely resemble the composition of the social microbiome. The arrow indicates an instance of migration. Upon entry and assimilation into the new network, the migrant's microbial composition changes as a function of both its intrinsic resilience and its social position in the new group (shown here by the green→blue shading).

microbial world, the probability of a microbe transmitting from one host island to another depends on more complex and dynamic measures of connectedness between host islands, arising from their movement [22]. Whilst many geological islands do indeed move over several millions of years (indeed, river islands can move, merge, and break apart on even faster time scales [145]), most animal host islands are vastly more mobile. Microbial acquisition amongst animal hosts can occur through various behavioural channels, including habitat selection [146], diet selection [124], probiotic use [147], or coprophagy [133–135].

Host islands are social, but geological islands are not. A significant proportion of the influence of host mobility on microbial transmission arises from host sociality. Thus, host sociality can be considered a special case of host mobility. Much social behaviour typically involves nonrandom movement towards or away from other hosts. When hosts approach or avoid specific individuals or groups, they also select for the microbes transmitted through these interactions. Many animals make social choices based on the potential for microbial transmission, for example, by selectively avoiding close contact with diseased conspecifics [148] or seeking exposure to maternal symbionts soon after birth. As an example of the latter, juvenile stinkbugs, young iguanas, and foals have been observed to selectively seek and consume adult faeces with the apparent aim of acquiring beneficial gut microbes [133–135]. The extent to which adult animals seek specific social interactions to modify their microbiomes is an interesting direction for future research.

Box 5. Dispersal may influence species abundances more strongly on geological islands than on host islands

On a geological island, metacommunity theory predicts that the abundance of a species is influenced by rates of immigration and emigration [30]. Host islands may present a somewhat different ecological scenario: though transmission can introduce a microbial taxon into a host, its subsequent abundance likely depends mostly on its growth rate within the host. Thus, transmission may be expected to primarily influence the presence rather than the abundance of a microbial taxon. In other words, transmission may be less central to species abundance on host islands compared to geological islands. Supporting the general hypothesis that species abundances are less affected by immigration in microbial systems compared to geological islands, studies of wild mice in natural social networks have shown that signals of microbial transmission can be better captured by measures of microbial presence–absence than abundance-weighted microbiome similarity [39,127]. However, these patterns have not been compared across species or different transmission ecologies, and future research efforts could entail experiments designed specifically to test the extent to which transmission can influence the abundance of specific gut microbes. Similarly, due to clonal growth, microbes moving out of the ecosystem may not appreciably deplete the abundance of their source population. For instance, whilst some estimates do suggest that bowel movements may cause the transient loss of one-third of the colon's microbial biomass [128], the long-term composition of the gut microbiome is probably only minimally influenced by these dynamics.

There are also some scenarios in which geological islands and host islands may resemble one another more closely than we have proposed to occur typically. For instance, on extremely remote islands where there is limited immigration or emigration, the abundance of a given taxon would depend heavily on the growth rate, making geological islands more similar to host islands. Conversely, there are cases where host islands are more similar to geological islands in terms of the outsized role that some microbial immigrants may play in the abundance of certain species. Some host islands may experience rampant *in situ* growth of ecosystem invaders, leading to infection and illness. Alternatively, consuming substrates very rich in specific bacteria (e.g., coprophagy or consuming probiotics or fermented items) may lead to increases in the abundance of those bacteria. However, these effects on abundances are probably transient [129].

Box 6. Two further comparisons between host islands and geological islands in terms of species movement between islands

Species inhabiting the sea between host islands can colonise islands more readily than species inhabiting the sea between geological islands

Unlike the sea between geological islands, the 'sea' between host islands does not comprise an unequivocally inhospitable habitat [19]. Amongst geological islands, the sea contains organisms that are unlikely to colonise the land habitat due to strong water–land niche separation. For host islands, the sea between islands is teeming with microbes, some of which can and do colonise the host islands [19]. For instance, some soil microbes can spread to animal guts [130], as can microbes inhabiting dietary substrates [124]. Furthermore, some specialist gut microbes can spread between hosts via shared environments [127]. The extent to which gut microbes can survive in the oxygen-rich external environment varies based on their possession of adaptations for endurance, including aerotolerance and sporulation mechanisms. For terrestrial host animals, anaerobic microbes may well experience their host islands as finches might experience a geological island—a habitable patch surrounded by uninhabitable matrix. In contrast, aerotolerant, sporulating microbes, capable of persisting in the oxygen-rich extra-host environment, may experience a much more continuous landscape, more analogous to valleys amidst hills than islands in the sea. In line with this possibility, a recent study in wild mice found that aerotolerant, sporulating gut bacteria were better able to transmit to new hosts through the environment, whereas anaerobic bacteria required intimate social contact to spread between hosts [127]. Similarly, gut microbes transmitting via close social contact between baboons were enriched in anaerobic taxa [119], whereas aerotolerance and transmissibility without close social contact were higher amongst aerotolerant and sporulating members of the human gut microbiome [118].

Species inhabiting geological islands disperse between more similar islands than microbes inhabiting host islands

Environmental conditions on geological islands, such as temperature, precipitation, and soil chemistry, show extremely strong spatial autocorrelation. That is, islands closer in space have more similar environments. Thus, species dispersing between spatially proximate geological islands tend to arrive in communities that are very similar to the ones from which they emigrated. Microbiomes spreading across individuals of a single host species will also arrive in relatively similar communities (given the general similarity between host islands of a single species). However, when microbes spread between hosts of different species, high connectivity does not imply similar within-host environments. Interspecies microbial transmission is a frequent occurrence [21], particularly between host species with strong ecological connections, such as humans and their pets [131], predators and their prey [40], and sympatric species [132]. The gut environment can differ markedly amongst these host islands, limiting the establishment of many incoming microbes. Thus, compared to geological islands, microbes on host islands, under conditions where interacting hosts comprise different species, experience a much more heterogeneous archipelago—perhaps analogous to having a tropical rainforest island neighbouring an arctic tundra island.

Box 7. Host control over microbial transmission

Mechanisms of host control extend to control over the microbes they acquire from external reservoirs via transmission. Hosts alter their foraging, social, and spatial behaviour, which in turn alters their microbial exposures and the microbes they acquire via various transmission modes. For instance, as discussed in the main text, juvenile stinkbugs, young iguanas, and foals all consume the faeces of adults seemingly to gain beneficial gut microbes [133–135]. Hosts may also shape microbial transmission by avoiding or seeking nutritional opportunities with specific odour or taste profiles. For example, the preference for sour flavours is rare in mammals but is present in primates, rats, and pigs, and may help them to consume lactate-producing bacteria important for digestion [136]. One of the most important ways of controlling microbial transmission is probably via specific social behaviours, because intimate social contact spreads microbes that are otherwise difficult to transmit. For example, koala parents produce a special type of faeces ('pap') which is consumed by their offspring soon after birth and prepares them for the dietary transition from milk to toxin-containing eucalyptus leaves [137]. Similarly, trophallaxis amongst termites [138] and mouth-to-mouth interactions in humans and other mammals have been suggested to have evolved in part to facilitate microbial transmission [139].

A significant proportion of host control over its microbiome occurs via coordinated control over both transmission and subsequent selection of incoming microbes. For example, mammalian mothers remodel their vaginal microbiomes towards the end of pregnancy, thereby regulating which microbes they transmit to their offspring during birth [140]. This control over transmission is then followed by selectively facilitating the growth of beneficial (possibly maternally transmitted) microbes through oligosaccharides [141] and immunoglobulins [142] in the mother's milk.

As young mammals develop, they become less dependent on their mothers, and their microbiomes can increasingly be shaped by social transmission, whilst the effect of maternal transmission declines [143]. At the same time, the mammalian gut becomes increasingly anoxic as it matures [144], which aids in the selection of microbes capable of fermentation. Because the most socially transmissible microbes tend to be anaerobes [119,127], this may help developing hosts retain these socially acquired symbionts.

The extent to which hosts are able to combine or coordinate their control over microbial interactions within the microbiome with their control over microbial transmission from other hosts remains unknown and is an interesting direction for future research. For example, do hosts selectively seek microbes that might outcompete a pathogen or pathobiont? Do hosts seek probiotics to facilitate the growth of beneficial microbes?

These kinds of social preferences for microbial transmission supply an important example of how hosts can exert control over their microbiomes beyond physiological selection. In contrast, geological islands do not selectively avoid or facilitate dispersal by potential colonisers.

Moreover, because most anaerobic, nonsporulating gut microbes spread via social interaction [118,127], social interaction comprises a key process shaping gut microbial transmission and composition. Social interaction plays an important role in microbial transmission between individuals, as abundantly demonstrated by research on humans [13,22,118–122], other group-living primates [119,149], and even mammals that do not live in well-defined groups [39] or are solitary [150]. Because social interactions function as dispersal channels for microbes between host islands, the transmission landscape of each microbiome is nested within the social network of its host [22]. Network science supplies a large toolkit to model microbial transmission along the complex and dynamic connectivity landscapes produced by social networks [119,126,127] (discussed later in this review).

Stochastic effects on geological islands and host islands

Stochasticity (ecological drift) refers to random fluctuations in local species abundances and regional dispersal patterns, which can drive both extinctions and introductions of species in communities. In line with the theory of island biogeography, smaller communities typically experience higher local stochasticity, predicting higher local extinctions and consequently lower numbers of species on smaller islands [151]. This positive correlation between island area and species diversity has been extensively documented in macroscopic communities inhabiting geological islands [28,42,152,153]. Paralleling this pattern, the size of host islands (body size) has also been associated with higher gut microbiome diversity across vertebrate species [44,45] and even between humans of varying heights [46]. Moreover, growth in body size with age during early life into adulthood (excluding senescence) may be associated with decreasing stochasticity in the gut microbiome. Indeed, evidence for reduced stochasticity and stronger local deterministic processes (species interactions and local selection) across ontogeny during physical growth are observed in the gut microbiomes of zebra fish [109], baboons [154], and humans [155]. Of course, any effect of growth (and greater available space) during this period will likely occur alongside maturation of the immune system [155,156], which stabilises the microbiome and limits stochastic fluctuations. As such, we should consider the stochasticity-reducing effects of increases in host body size as a speculative mechanism that accompanies and augments the stochasticity-reducing effects of immunity and other host factors. Furthermore, whilst immunological immaturity allows greater microbiome stochasticity on young host islands, immunosenescence may also permit increased microbiome stochasticity amongst older hosts, as the strength of immune-based negative feedback mechanisms declines [157].

Unlike geological islands, stochasticity in the microbiome—often linked with various ‘dysbiotic’ states—can be deleterious to host survival and reproduction [17,104]. Such detrimental effects drive the evolution of host control mechanisms that limit stochasticity. Perhaps for this reason, host-associated microbiomes, particularly those of vertebrates (which possess adaptive immunity), are remarkably stable compared to free-living microbial communities [158,159].

Microbiomes as metacommunities in social networks

Because gut microbes spread between hosts via social interaction, microbiome metacommunities are nested within host social networks (Figures 2 and 3). When microbes spread through different types of social contact (e.g., parturition, mating, grooming, incidental touch, or sharing space), microbial transmission pathways can be described using a set of parallel networks between the same nodes in the form of a **multilayer network** [22,160]. Social connections differ mathematically from geographic distances in some crucial ways. For example, social interaction is noncontinuous in time. Social networks are also sparse, meaning that any two nodes need not necessarily share a direct connection but are instead connected via indirect paths through other nodes in the network. Thus, modelling microbial transmission in social networks requires more complex and dynamic measures of connectivity than the spatial distances often employed in metacommunity ecology. Moreover, the transmission of commensals and mutualists tends to differ from the transmission of pathogens (in that it is a bidirectional process of whole-community homogenisation). Because of this, the transmission of microbiome members is not particularly amenable to description by classic epidemic models that trace the directed spread of single agents across a network. Nevertheless, insights from broader network analysis, especially diffusion processes, can be useful for understanding transmission across microbiome metacommunities. For example, tools from network analysis that recognise local and global network structures can help us build metacommunity models that describe both the effects of the rate of microbial dispersal and also how the structure of the dispersal network influences local and regional diversity in microbiome metacommunities. Similarly, models of **jump-diffusion processes** [161] can be useful in describing **social transmission** where social interaction is temporally sporadic.

We summarise three ways in which considering microbial transmission as a network phenomenon can reveal ecological patterns that would remain hidden under more traditional models of dispersal in island biology (Figure 4).

Effects of direct and indirect social transmission on the microbiome

Connectedness between host islands in a microbial metacommunity network is not only captured by simple measures of pairwise distance or contact (Figure 4A) but also by indirect

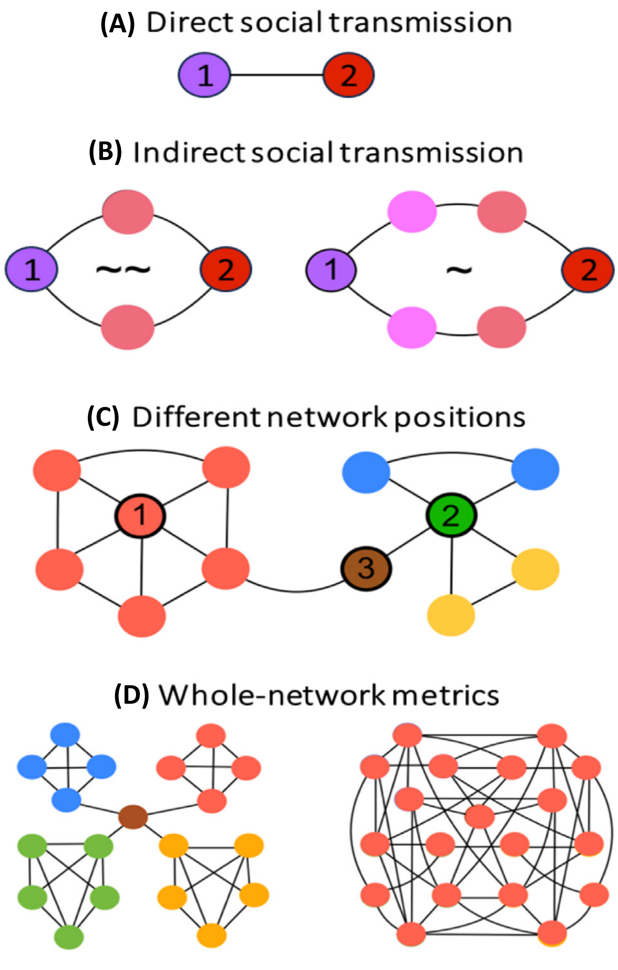

Figure 4. Emergent network phenomena that can influence compositional patterns in a metacommunity. (A) Direct social transmission may homogenise the microbiome communities of two interacting hosts. (B) Indirect social transmission through intermediate nodes may also homogenise microbiome compositions. The strength of this homogenisation decreases with a growing number of intermediate steps between nodes. Here, the compositions (colour) of node 1 and node 2 influence one another indirectly by transmission via intermediate nodes. Consequently, their compositions are more similar to one another (~~) when the number of indirect steps between them is small, and less similar (~) as the number of indirect steps increases. (C) Different network positions can drive individual subcommunities to accumulate different emergent community compositions. Here, node 1 and node 2 possess different centrality properties. Whilst they both have a degree of five (five direct links), node 1's position in the network is described by high transitivity (a high level of interconnected connections), whilst node 2's position is best described by high betweenness (high levels of connections to otherwise disconnected parts of the network). These network processes affect the mixing of community compositions (colours) in a metacommunity, here represented with more similar colours depicting more similar communities and compound colours (green, brown) depicting more diverse communities than primary colours (red, yellow, blue). Specifically, as node 2 is exposed to transmission from more distinct subcommunities in a metacommunity, it gains elements from all of these distinct sources, leading to higher overall diversity (blue + yellow = green). Under this scenario, the most diverse community in this network accumulates in node 3 (brown), which connects to the highest number of distinct sources, a position best described by high bridge propensity (high distinctness of connections relative to the number of connections). (D) Whole-network metrics may shape the global compositional patterns of a metacommunity. For example, compared to highly interconnected networks (right), more modular networks (left) may harbour higher global diversity (γ-diversity), represented by a greater number of colours. This is due to both the enriching effect of isolation (chance variation arising in separated local subcommunities) as well as the enriching effect of connectedness (internode and intermodule connectedness rescuing species from chance extinctions).

connections through intermediate host islands (Figure 4B). Mirroring this phenomenon, recent evidence from humans and other animals has highlighted the importance of considering indirect connections in a social network to explain microbiome variation [22,122,162]. This is conceptually similar to the **stepping-stone model** of colonisation on geological islands [163]. Future research might examine how cryptic exposures to microbes from individuals and groups to which one is not directly connected can maintain microbiome diversity.

Effects of individual network position on emergent community properties of their microbiomes

Many of the health benefits of microbiomes are based on emergent community properties of the microbiome as a whole, such as its diversity or stability [16,26,158,164,165]. In metacommunity ecology, these emergent community properties have been linked to the local connectedness of subcommunities [35]. For instance, local diversity on a geological island is expected to be highest at intermediate levels of connectedness [166].

In addition to a continuous scale of low to high connectedness, these transmission landscapes can be defined using the rich set of centrality metrics from network science that describe different network positions. For example, an individual's position in a social network can be summarised through measures of network degree (number of connections), transitivity (how connected an individual's connections are to one another), or betweenness (the extent to which an individual bridges otherwise disconnected parts of the network) [167]. By predicting emergent microbiome properties such as diversity or stability with these nuanced measures of a node's position in a microbiome metacommunity network, we can gain insight into what kinds of contact landscapes support healthy diversity or stability in a microbiome (Figure 4B). For example, gut microbial diversity has been shown to correlate positively with social network degree (an individual's number of unique social partners and contacts) in lemurs [126], chimpanzees [149], and humans [168]. Conversely, gut microbial diversity has been found to be negatively correlated with social network strength (the total amount of time spent in social interactions) in lemurs [169] and marmots [170]. Further, amongst wild mice, microbiome richness was influenced by the nature of the centrality of the host within their social network, with mice possessing a high bridgelike centrality (e.g., betweenness) displaying more diverse microbiomes than those with high clusterlike centrality [39]. This is likely because connections from distinct parts of the network may transmit different microbes to the focal individual. Researchers could further assess which local network positions are most diversifying, stabilising, or homogenising for the social microbiome of an animal population.

Effects of whole-network structure on properties of the total microbiome metacommunity

Properties of a whole metacommunity are influenced by the overall connectedness between subcommunities. For example, the general loss of connectedness between habitat patches, resulting from anthropogenic landscape fragmentation, is driving biodiversity loss in macroscopic ecosystems [171]. Similar links between microbiome composition and the social network structure of the host likely play a significant role in shaping the global properties of microbes that transmit amongst hosts [21]. Considering microbiomes in metacommunity networks will enable researchers to understand what other meaningful clusters beyond single hosts—such as those created by social groups—may exist in this microbial metacommunity (Figure 4C). Furthermore, this perspective allows us to ask how different social systems result in distinct social microbiomes. In this vein, a hierarchical society might result in source–sink dynamics, similar to those occurring in macroscopic communities where prevailing winds define a specific direction for the colonisation of rock pools by aquatic invertebrates [172]. For instance, a high-ranking member may act as a **species source**, with microbes moving down the hierarchy to colonise a low-ranking member (which acts as a **species sink**), or vice versa.

A logical next step in microbial transmission research will be to link the structural properties of the social networks (e.g., network modularity and connectivity) to whole metacommunity properties (e.g., a host population's microbiome ***γ*-diversity**, and overall stability) across different host species or populations. This will permit us to investigate matters such as the kinds of social structures that maximise microbial diversity, stability, or resilience within a population (Figure 4D).

Eco-evolutionary metacommunity dynamics on geological islands and host islands

Evolution in a metacommunity is influenced by the interplay between locally varying selective conditions and regional dispersal, which changes these selective pressures by altering community composition. For example, in a metacommunity system of gall flies and their parasitoids, flies faced differential parasitoid-related selective pressures on different patches and consequently evolved reduced dispersal capacity on more isolated patches to maintain local adaptations to local parasitoids [173]. Conversely, species can also escape local antagonistic interactions and become invasive by dispersing onto islands lacking their natural enemies [174]. Similarly, gut microbes may possess a selective advantage when spreading into communities that lack their competitors or specialist bacteriophage predators.

A key aspect of how ecological and evolutionary processes interact with one another is their relative speed. In macroscopic systems, rates of ecological change are usually higher than rates of evolutionary change, though rapid evolution can also occur on ecological timescales [175]. On host islands, both processes tend to be swifter because microorganisms evolve faster than macroorganisms [176] and ecological conditions within a host change rapidly due to variation in host physiology [1]. It could also be interesting to consider the lifespan of host islands relative to geological islands: although the absolute spatiotemporal scales of geological islands and host islands differ markedly, the ratios of lifespans between islands and their species may not be far from the ratios of lifespans between hosts and their microbes. If species inhabiting geological islands have generation times ranging between 1–10 years, and island ages range from thousands (e.g., Baltic Sea islands) to millions (e.g., Hawaiian islands) of years, the ratio of generation time to island age would overlap with similar ratios on host islands, where bacteria may divide every ~20 minutes to 10 hours within hosts that live for 1–100 years. This suggests that some of the insights into eco-evolutionary dynamics garnered from geological islands may be relevant for host islands. For example, host islands could be compared to volcanic hotspot islands of the Hawaiian Archipelago, where the effect of continental drift over a mantle hotspot leads to the formation of a new island approximately every one million years [28,177]. These islands are colonised by species from nearby islands and gain diversity through dispersal and local evolution, producing a clear biodiversity gradient in the differentially aged Hawaiian islands [178]. This is reminiscent of the bioaccumulation of more diverse microbiomes across time in developing and ageing hosts, where adaptive evolution of bacterial lineages can occur over a human lifetime [179]. One difference between geological and host islands in this regard is that, whereas the Hawaiian islands have evolved entirely new species and even genera, microbial divergence within the host's lifetime is measured at the scale of strains [179–181]. Moreover, **horizontal gene transfer** amongst bacteria can facilitate rapid evolution of new functional diversity, and provides an alternative route for rapid *in situ* evolution. This is exemplified by the swift evolution of antibiotic resistance via the acquisition of resistance genes by microbes unexposed to antibiotics [182].

In addition to evolutionary rates, a key difference between eco-evolutionary metacommunity dynamics on geological and host islands lies in the instability of the islands themselves. Whilst geological islands tend to persist irrespective of the dynamics characterising their constituent communities, host islands both emerge rapidly through reproduction and disappear rapidly via death in ways that are influenced by their microbial inhabitants. For example, variation in the gut microbiome has been linked to survival in free-living Seychelles warblers (*Acrocephalus sechellensis*) [183], meerkats (*Suricata suricatta*) [184], and feral horses (*Equus ferus caballus*) [8]. Furthermore, gut and reproductive microbiomes have also been linked to fertility in both sexes in humans and nonhuman animals [185,186]. Thus, gut microbiomes can remodel existing host phenotypes or confer novel functions to influence host fitness [101,103].

Reciprocal relevance of island biology and microbiome science

We have demonstrated a range of similarities and differences between geological islands and host islands. The principal similarity is that, like geological islands, host-associated microbiomes are fundamentally shaped by metacommunity processes occurring across various ecological scales (Figure 1). However, we have also illustrated several crucial differences between geological and host islands, most notably those attributable to host movement and adaptive evolution, which are irrelevant considerations for geological islands. We caution against ignoring these differences, which would be tantamount to overextending the host-as-island metaphor and reducing the host microbiome to a special case of island biology. Rather, tailoring models of island biology to account for these differences will more effectively enhance microbiome science.

Metacommunity models have already proved extremely useful in explaining microbiome variation. For instance, researchers have exploited metacommunity models to demonstrate how the main influences on gut microbiome composition change over ontogeny: early in zebrafish development, for instance, microbiome composition is strongly influenced by microbial transmission, whereas later in development, microbiome composition becomes more a matter of host control [109]. Similarly, island biology has been useful in understanding how the microbiome is influenced by transmission and within-host selective forces differentially in western and nonwestern human societies [187].

Models of microbiome ecology that consider processes occuring both within hosts (e.g., models of microbiome ecological networks) and between hosts (e.g., metacommunity models of varying local selection and microbial transmission) have yielded insights of biomedical relevance. For example, models of island biology have enhanced our understanding of clinically important microbiome variation along regions of the human lung [188] and skin pores [189] (Box 2). Similarly, models of colonisation resistance amply highlight the biomedical value of ecological views of the microbiome [190]. For example, understanding that pathogen-mediated disease depends on local competition in the microbiome, in addition to the intrinsic invasive tendencies of the pathogen, has transformed our ability to model pathogenesis. Updating metacommunity models to simultaneously reflect all four metacommunity processes will likely further advance clinically important microbiome discoveries. Indeed, many diseases can be understood in terms of the ecology of the microbiome, including colonisation resistance of the resident community [25,26]. Thus, after a century of studying systemic immune function and the spread of disease, we are now poised to begin considering the systemic emergence of pathogenesis and the spread of resilience against disease as properties of the microbiome [22,117]. As just one example, elucidating the ecological influences on microbiome composition may help in understanding the various ways in which the microbiome alters risk and resilience to viruses such as SARS-CoV-2, which could in turn aid in disease management and potentially even pandemic preparedness [191].

Alongside utilising island biology to understand microbiomes, microbiome science can also enhance our understanding of island biology. For instance, the application of network models, developed to understand microbial transmission [119,127], could prove useful as extensions to the models of stepping-stone type connectivity on geological islands. These metacommunity networks could lead to new insights into the kinds of connectivity that matter most, where macroscopic biodiversity accumulates in a network of interconnected communities, or what positions in a network promote community stability or vulnerability. In addition to methodological advances, microbiome ecology also offers tractable study systems for the empirical investigation of long-standing questions and hypotheses in theoretical island biology. These theories have been challenging to study experimentally owing to the difficulty of tracing the within-community dynamics and between-community movement of many macroscopic species simultaneously over substantial timescales. On host islands, the relevant processes could be studied over the entire island lifespan in a matter of months to years—processes that could last tens of millions of years for geological islands. For example, research on microbial metacommunities inhabiting water-filled tree holes has demonstrated that the tendency of larger islands to host higher diversity holds for microbial ecosystems as well [43]. Investigations of microbial metacommunities has also revealed that dispersal and local selection interact to limit local adaptation [192]. Studying the microbiomes of animal hosts such as nematodes, fruit flies, zebrafish, or mice allows even more detailed experimental manipulation of all four metacommunity processes (Figure 1). For instance, transmission networks can be controlled by cohousing hosts [193], and the level of host-induced selection and stochasticity can be manipulated using host individuals with varying levels of immunosuppression [194] or other ecologically relevant phenotypes. Even the ecological interactions amongst microbes can be modified by experimental evolution of microbial strains [47]. Furthermore, germ-free animals provide tractable systems to explore the very first stages of island colonisation, which are virtually impossible to study on geological islands.

Concluding remarks

Biology is replete with metaphors. The present effort illustrates that it can be fruitful to analyse a metaphor to better understand its strengths and limitations, which can, in turn, aid scientific inquiry [49]. We have examined the host-as-island metaphor to develop an understanding of how the ecology of species communities inhabiting animal host islands may (and may not) be comparable to those inhabiting geological islands. In particular, we have studied the similarities and differences in the actions of the four central metacommunity processes in both host and geological islands: species interactions, local selection, transmission, and stochasticity (Figure 1). This effort may also assist researchers in accounting for much of the unexplained variance in microbiome composition and diversity across a broad range of hosts. The proportion of microbiome variance explained by each of the four metacommunity processes is presently unclear and could be a useful starting point for future research. Much else remains to be done (see Outstanding questions). Ultimately, the goal of understanding microbiome variation, for both biological interest and biomedical translation, can only be realised by studying the microbiome as a dynamic ecosystem operating under metacommunity processes [14]. To achieve this, models of island biology will need to be updated to reflect the ecological reality of microbiomes.

Outstanding questions

What proportion of the variation in the animal gut microbiome is attributable to each of the four metacommunity processes (within-host microbial interactions, within-host selective effects, transmission, and stochasticity)?

What is the relative contribution of the different metacommunity processes to microbiome community assembly and composition at various sites on or within the host organism (e.g., gut, skin, oral cavity, genitals, and specialised organs)?

How do interspecific differences in host habitat, social structure, and physiology (e.g., gastrointestinal tract length and immune function) influence the balance of within-host microbial interactions versus within-host selective effects versus interhost transmission versus stochasticity?

What kinds of positions in the social network maximise microbial biodiversity?

Are there some social network structures that impose dispersal limitations strong enough for microbial lineages to evolve into separate strains in different hosts?

Do pathogenic and mutualistic microbes possess different transmission dynamics due to the differing levels of within-host selection they encounter as they spread?

What is the relative importance of ecological processes (within-host microbial interactions, host selection, transmission, stochasticity) in facilitating adaptive microbiome responses in the short term, and the maintenance of adaptive microbiome variation in the long term (across host generations)?

How can the current framework be expanded to account for sessile animals, as well as other organisms such as plants?

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