Microbial Transmission in Animal Social Networks and the Social Microbiome

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Abstract: Host-associated microbiomes play an increasingly appreciated role in animal metabolism, immunity, and health. The microbes in turn depend on their host for resources and can be transmitted across the host's social network. In this article, we describe how animal social interactions and networks may provide channels for microbial transmission. We propose the 'social microbiome' as the microbial metacommunity of an animal social group. We then consider the various social and environmental forces that are likely to influence the social microbiome at multiple scales, including at the individual level, within social group, between groups, within populations and species, and finally between species. Through our comprehensive discussion of the ways in which sociobiological and ecological factors may affect microbial transmission, we outline new research directions for the field.

All known multicellular life has hosted microbial life throughout evolutionary history[1]. There is growing evidence that microbial symbionts may impact the normal development and function of host physiology[2], metabolism and immunity[3-6]. The microbiome also contributes to the production of bioactive molecules from the fermentation of otherwise non-digestible polysaccharides[7], synthesises vitamins[8], and regulates the biotransformation of a range of xenobiotic compounds[9,10]. Researchers have also become interested in microbial effects on the host's central nervous system[11], and how these may in turn influence behaviour[11-16].

Gut microbiome composition is affected by both the host's genes and its lifestyle, including diet and interactions with the external environment[17-22]. Among these environmental effects, the host's social environment and interactions are emerging as significant factors influencing microbiome composition[23-25]. Group living is common in the animal kingdom[26], and its benefits include reduced predation, enhanced mating success, enhanced wellbeing and longevity from social bonding, and assistance in rearing infants. However, group living can also have costs, including the suppression of reproduction in subordinates, aggression from higher ranking members, increased scramble competition, lower offspring success for low-ranking members, infanticide by other group members or immigrants, and pathogen transmission. Nonetheless, for group living to have evolved, its benefits must, on average, have outweighed its costs.

Since group living provides routes of transmission for microbes via animal social interactions, it may have important effects on microbial composition. However, variation in the microbiome within and between species likely depends on variation in the structure, strength, and stability of social connections. In this article we synthesize evidence of microbial transmission across animal social networks. We then propose the concept of the 'social microbiome', which we define as the collective microbial metacommunity of an animal social group or network. A metacommunity refers to a set of biological communities that interact with

one another via the movements of species between those communities (e.g. birds between islands, or microbes between hosts[27]). The social microbiome provides a lens through which to conceptualize the links between host sociality and individual microbiomes, synthesizing research across multiple scales—from single organisms to species-level and interspecific interactions. We place considerable emphasis on primates, since primate societies have provided some of the strongest evidence for socially transmitted microbes in mammals[25,28], though our framework is relevant to all social animals. We concentrate mainly on the gut microbiome, but the concept that social interactions shape the microbial metacommunity is applicable to microbial communities at multiple body sites.

The Social Transmission of Microbes

If ecological metacommunity theory[27] and island biogeography theory[29,30] are applied to microbial transmission, individual hosts can be interpreted as 'islands' (or 'patches') that are habitable by gut microbes[31]. These islands are interspersed across an oxygen-rich external environment that is hostile to many host-associated gut microbes, which must therefore rely on efficient means of moving between and colonising hosts[31]. Host social interactions can provide opportunities for direct and indirect microbial transmission between hosts, and thus contribute to shaping the microbial metacommunity of a social group[32-34].

Indeed, applications of metacommunity theory to microbiome research have gained significant traction in the last few years, providing valuable conceptual frameworks for understanding microbial assembly and dispersal[31,35-40]. Under this framework, an animal social network represents a set of islands or patches (hosts) linked by social connections that enable the transmission of microbes. Whilst the transmission of parasites and pathogens within animal social networks has been extensively researched[41-43], the social transmission of commensal and beneficial microbes has only recently garnered significant attention[23,44].

Social transmission of microbes may be mediated by physical social contact (e.g. grooming) and behaviours such as parent–infant feeding, mouth-to-mouth interactions, and coprophagy (i.e. ingesting faeces). Transmission of microbes between individuals in a social group may provide important health benefits to hosts. For instance, gut microbes (including those acquired via social interactions) have recently been found to reduce susceptibility to the protozoan parasite *Lotmaria passim* in honeybees[45]. Similarly, gut microbes acquired from nestmates also protect social bees from infection by *Crithidia bombi*[46], whilst solitary bees lack these gut microbes[47] and therefore suffer more acutely from this parasite. Indeed, some researchers have theorised that acquiring beneficial microbes may have been a factor contributing to the evolution of sociality[48,49]. Below, we summarize evidence of the social effects on the microbiome in captive settings and also in natural populations of primates, including humans (see Box 1 for a description of social transmission of microbes in laboratory settings, or 'cage effects').

Social Transmission of Microbes in Natural Populations of Nonhuman Primates: In the last few years, researchers have begun investigation the social transmission of commensal microbes has been in wild primates. A study of microbiome composition in two baboon groups, controlling for variation in diet, environment, and genetic relatedness, provided evidence that gut microbes are transmissible via physical contact between social partners[50]. Notably, group membership was a better predictor of the composition of an individual baboon's gut microbiome than either age or sex. Compositional similarity between microbiomes was associated with grooming between baboons, even after controlling for shared environments, diets, and genetic similarity[50].

Further research on this baboon population investigated the social transmission of core and non-core microbes[51]. Core microbes are, by definition, found in the majority of hosts in a population[52] and perform essential services for the host, such as vitamin biosynthesis and the

breakdown of otherwise non-digestible plant polysaccharides. Non-core microbes are thought to represent transient environmental exposures, and may therefore be expected to exhibit stronger signatures of socially mediated transmission, as compared to more prevalent core microbes. The researchers predicted that only non-core microbes would be sensitive to social structure[51] but surprisingly, both core and non-core microbes exhibited signatures of social transmission. These results indicate that social effects on microbiome composition are not restricted to transient, environmentally acquired microbes, but may be pervasive across the microbiome and thus affect microbiome function.

A study of chimpanzees also found that social interactions among hosts promoted both gut microbiome richness and similarity in a social network[53]. Bacterial species richness of individual gut microbiomes covaried positively with the degree of sociability among chimpanzees. Furthermore, infant gut microbial communities displayed a stronger signature of social transmission than vertical transmission of microbes from the mother[53]. These results indicate that social transmission in primates may help maintain bacterial composition and species richness across generations. Similar patterns have been observed in lemurs, with the degree of grooming and sociability predicting the similarity of gut microbial composition even after controlling for the influence of diet and relatedness[54].

A link between sociability and gut microbial composition has also been observed in black howler monkeys[55]. These primates are arboreal and less social than more terrestrial primates, operating in smaller groups, and engaging in less extensive grooming[55]. Individuals that spent more time in physical contact or close proximity had more similar microbiome profiles, and the abundance of bacterial genera such as *Bacteroides*, *Clostridium*, and *Streptococcus* were more similar in monkeys that showed higher rates of interaction[55]. In general, the effects of sociability on microbial composition appeared to be smaller in howlers

than in baboons[50] and chimpanzees[53], which, as the authors note, is consistent with comparatively lower rates of social contact among howler monkeys[55].

Findings such as these suggest that primate social networks can act as conduits for microbial exchange within a host population. The strength and qualitative aspects of the social bond (measured, for instance, in the time that primates spend grooming one another, or which social partners a primate prefers) predict the similarity of microbial composition. This prediction was made some years prior to empirical investigations into the social transmission of commensal and beneficial microbes in primates[24,56-58]. Studies have now found evidence supporting this prediction, including in baboons[50,51], chimpanzees[53], howler monkeys[55], and lemurs[54,59], but such patterns have not been observed in mangabeys[60].

To date, most studies of social microbiota transmission provide correlational evidence, observing that close social partners or individuals living in the same group have more similar microbiomes than individuals who are not social partners or live in different groups. However, these patterns can arise not only from social contact, but also from transmission via shared environments, similar diets among group members, and host genetic effects on microbiome composition (i.e., the degree to which members of a group share genes). Although some studies have been able to statistically control for confounding effects of diet and genetic relatedness[50,53], there remains a need for controlled experimental studies that manipulate host social networks and observe effects on microbiota transmission directly.

Social Transmission of Microbes in Humans: The social environment also influences the human microbiome. For instance, humans sharing a household, including unrelated individuals, harbour more similar gut microbiomes than individuals in different households[61-63]. In addition, dogs appear to both acquire microbes from, and contribute microbes to, the microbiomes of their owners[62], suggesting that pets may also act as microbial transmission vectors between household members. A longitudinal study measuring the skin microbiomes of

families over several weeks found that regular social interaction resulted in more similar microbiome profiles, that composition was distinct between different households, and that microbial transfer was also mediated by household surfaces[61]. Furthermore, when a family moved from one house to another, the microbes found on the surfaces of the new house rapidly changed to reflect the skin microbes of the incoming family[61]. Similarly, the microbial content of household dust is influenced by the number and types of occupants within a household[64], as well as the presence of dogs[62,65]. Thus, individuals leave a microbial trace on the built environment which is transmissible to others sharing that environment. Indoor environments therefore likely serve as microbial reservoirs[61,66-69], which could facilitate microbial transmission between humans. Microbes may also be transmitted between humans directly through social contact. For example, an estimated 80 million oral bacteria are transferred in an intimate kiss lasting ten seconds[70]. A range of mouth-to-mouth interactions has been observed in other primates[24,48,71] and may also contribute to microbial transmission in these species.

While substantial attention has been paid to the social transmission of pathogens in humans[72], researchers have also recently begun discovering direct mappings between human social networks and the transmission of commensal and mutualistic microbes. Doing so requires linking social networks to gut microbial similarity, while controlling for dietary, environmental, and genetic similarity among hosts. One study that comes close to meeting these requirements found similar gut microbiota among married couples who ranked their relationships as especially close[73]. In contrast, the mean gut microbial similarity between married couples reporting lower levels of closeness was not significantly different from that of individuals living separately[73].

Another promising approach to demonstrating a causal link between social bonds and gut microbial transmission is strain tracking. This technique relies on population genetic approaches to infer the transmission of microbial strains based on single nucleotide variants in

high coverage shotgun metagenomic data. It has already been used to investigate the vertical transmission of microbes from mother to infant[74,75], but is also suitable for the analysis of horizontal transmission of microbes through social interactions. Monitoring the transmission dynamics of closely related bacterial strains requires metagenomic approaches with higher resolution than standard 16S rRNA gene sequencing[74,76]. In this vein, a recent investigation in humans inferred microbial transmission between social partners using strain tracking: the researchers found evidence of shared oral and gut microbes in social networks in Fijian communities, including between close social partners (mothers and infants, marital partners), as well as closer microbial sharing between females compared to males[77]. Furthermore, it has recently been found that individuals with larger social networks tend to have more diverse gut microbiomes[78]. This was the first study to investigate the relationship between sociability and gut microbiome diversity in humans, and supports previous findings in primates that social interactions promote microbial diversity.

Host Social Groups as Biological Archipelagos: The Social Microbiome

There has been considerable interest in studying hosts as islands[79,80]. In an early investigation of intestinal protozoan diversity amongst rainforest-dwelling primate groups, social groups were described as 'biological islands' where each group possessed a unique signature of intestinal protozoa that differentiated it from neighbouring groups[81]. This early attempt at differentiating social groups on the basis of parasites was prescient, and island analogies have been extended from parasites to commensal microbes. Indeed, social groups of the same species are frequently distinguishable on the basis of microbial composition, as shown in baboons[50], geladas[82], chimpanzees[60,83], mangabeys[60], howler monkeys[55], rhesus monkeys[84], capuchins[85], ring-tailed lemurs[86], colobus monkeys[87,88], Verreaux's sifakas[89], equids[90] and fur seals[91].

We use social microbiome as a shorthand term to describe the microbial metacommunity of all hosts in a social group. Our use of 'social microbiome' is consistent with the 'pan-microbiome' concept (the collection of microbes of a host species[52,92]) but places a social constraint on the microbial metacommunity based on the interactions occurring over time within a group and in the context of local ecology. Thus, the main aspect of the social microbiome as it relates to microbial metacommunities is the importance of being associated with a *specific social group or network*, rather than belonging to the species or population as a whole.

The social microbiome concept is consistent with the general framework of island biogeography and metacommunity ecology. From this perspective, the microbiomes of individual hosts within a social network can be considered islands within an archipelago (Figure 1). These islands harbour a metacommunity connected in part via the hosts' social network, such that microbial dispersal increases with increasing social connectedness between hosts. By altering the spatial structure of the islands (hosts), social interactions are expected to have cascading effects on the dynamics and diversity of the microbial metacommunity, as has been shown in theoretical and empirical studies of other metacommunities[33,93,94]. For example, proximity and connectivity are expected to decrease β-diversity between patches[32,34,93], a prediction that has been observed in experimental zooplankton metacommunities[33].

The primary benefit of considering the microbial metacommunity harboured by an animal social group is that it allows a metacommunity connectivity matrix to be defined explicitly by the social network. In contrast, if we ignore social constraints on interactions between conspecifics, members of a host species can be viewed as a large archipelago with a uniform spatial organisation amongst the islands, and little or no clustering (Figure 1, left side). In light of metacommunity theory, such an arrangement may be considered a spatially implicit model, in which the distribution of islands exerts no differential effects on the inter-island

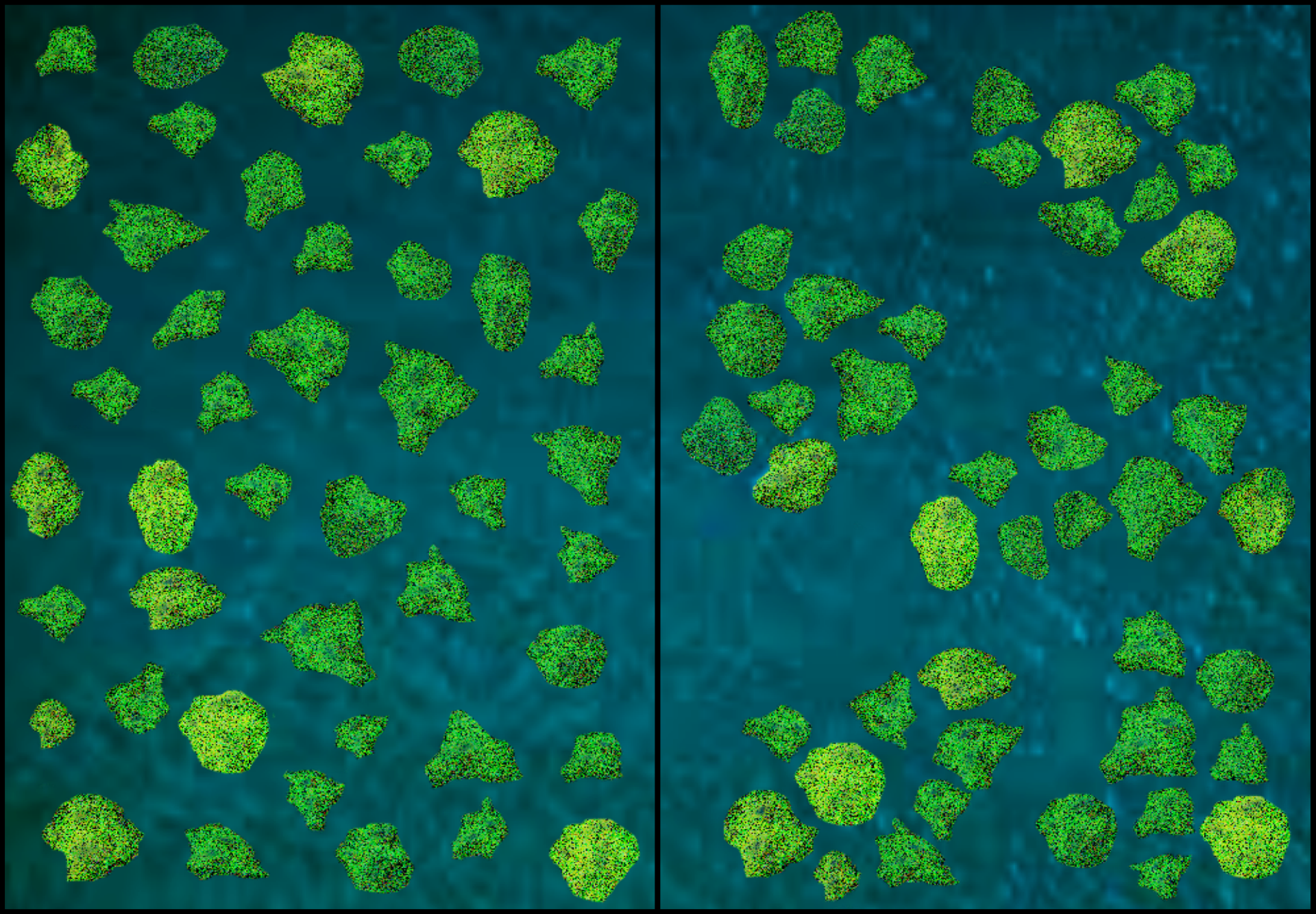

Figure 1 – Social Microbiomes as Biological Archipelagos: Each island represents a host that is colonised by microbes, and in group-living species these hosts form 'archipelagos' for microbes. The central question is how the arrangement of islands affects microbial dispersal between them. Metacommunity theory and island biogeography theory can be applied to both sets of islands shown here. On the left is a representation of a spatially implicit model which ignores the effects of space, represented by islands that are evenly distributed to convey the idea that migration is equally likely between all islands (note that it is not possible to represent spatial distributions in the implicit model using two dimensions). This model does not account for the intrinsic social organisation of many animal species. In contrast, the social microbiome concept places social constraints on the organisation of host populations, yielding the island structure on the right (multiple, spatially distinct archipelagos), consistent with the idea of a spatially explicit model.

Figure 2 – Processes at Different Scales Influencing the Social Microbiome. At each scale, processes can affect microbial dispersal and selection, both of which can affect microbiome structure and function within individual hosts. Levels 1 to 5 describe the effects of individual-, intragroup-, intergroup-, intraspecies-, and interspecies interactions on the social microbiome. Level 1 encompasses individual social interactions within a group. Level 2 describes group characteristics that influence Level 1 interactions. Level 3 considers interactions between social groups of conspecifics. Level 4 captures differences between populations or species and the effects of the physical environment. Level 5 describes interactions between host species that inhabit the same physical environment. All levels are hypothesised to influence the microbial metacommunity of a host social group.

Figure 3 - Effect of Immigration on the Social Microbiome: Here, we show two hypothetical meerkat mobs, with the orange and blue ovals representing two distinct social microbiomes. Within each mob, there is a dominant female (represented by the largest animal in each group). There are also smaller subgroups of individuals that may interact more frequently with one another, and collectively engage in rearing the dominant female's offspring. The group in between the two mobs represents a coalition migrating from the orange mob to the neighbouring blue mob (indicated by the orange-blue shaded arrow next to the group). During assimilation into the new mob, the migrants' microbial composition is expected to change as a result of microbial transmission via social interactions with the new group. In addition, we predict that as the number of migrating individuals increases, so does the effect on the social microbiomes of both the natal group (right hand side, lower graph) and the receiving group (right hand side, lower graph).

movement of species[27]. However, this lack of clustering of islands ignores the sociobiological reality that many animal species live in groups with predictable membership and differentiated social relationships. In contrast, if we account for the fact that social animals live in relatively structured groups, then we can instead view host social groups as a series of archipelagos (Figure 1, right side). Each archipelago, spatially separated from its neighbours, represents a host social group (with each island representing an individual host) and within social groups, hosts are differentially connected. Thus, the social microbiome can be represented by spatially explicit models in which the spatial distribution of islands is non-uniform[27]. Recent theoretical work has specifically examined the role of explicit spatial structure in archipelagos, finding that within-archipelago features, such as the arrangement of islands comprising the archipelago and distance between islands, are associated with appreciable variations in species composition and richness of individual islands[34,95,96]. Translating this theory to host social groups suggests that social groups could be viewed as units of analysis in terms of microbial richness, diversity, and dispersal, with social interactions and relationships between hosts affecting inter-host microbial transmission.

Focussing on the microbial metacommunity of a specific social group (i.e. the social microbiome) allows us to form hypotheses regarding how an individual's position in a social network may influence its microbial composition. The gut microbial community in any individual host can be interpreted as a variant of the social microbiome, deviating from the average gut microbial composition of the group due to the host's position in the social group, as well as other host-specific traits that influence microbiome composition (e.g. diet, age, health status, genotype, reproductive status).

Using of the social microbiome concept, we can consider the properties and dynamics of the microbial metacommunity and how social interactions may influence microbial transmission between individuals, with implications for host health and physiology. For

instance, if we define the social microbiome as a metacommunity, this metacommunity should be more stable and resilient than any individual microbiome in the network. The stability of the microbiome describes the capacity to retain its compositional state in response to disturbance, while resilience refers to the rate at which it is able to return to this pre-disturbance state[97,98]. A stable and resilient social microbiome may also help promote stability and resilience of an individual's microbiome. As may be expected, studies have revealed that instability or low resilience of the gut microbiome are often associated with poor health[97-101].

Social and Environmental Forces Acting on the Social Microbiome

Using standard principles from metacommunity ecology, we propose that several processes may be operating simultaneously at different scales within and between animal societies to influence the structure and stability of the social microbiome (Figure 2): 1) individual host-level processes, 2) group-level processes , 3) between-group processes, 4) lifestyle and species-level characteristics operating at the level of host species and populations, and 5) interactions between sympatric species. At each scale, these processes have the potential to affect microbial dispersal between hosts and selection within individual hosts, thereby shaping the composition and function of individual microbiomes. Across levels, the strength of microbial colonisation from the host's social and physical environment will be balanced against the host's control of its microbiome. The relative strength of these forces across levels will affect the characteristics of the social group's microbial metacommunity.

It should be kept in mind that several of these processes occur on multiple scales. For example, the sex distribution within a social network, which we describe in the context of group-level processes (Level 2), is also relevant as a species-level process (Level 4) given sex ratio variations across species. We illustrate each level with examples largely from the gut

microbiome, although the social microbiome concept is expected to hold for microbial communities at any body site.

Level 1 – Individual Host-Level Processes: Individuals differ dramatically in the number, strength, and nature of their social connections. These quantitative and qualitative aspects of social contact vary depending on the individual's age, sex, role, and dominance rank in the group. These individual-level factors can influence social interactions and therefore microbial transmission within a network, affecting the microbiomes of individual hosts differently based on their connections in the group. The potential for microbial transmission between group members will be influenced by at least two aspects of social contact: the physical intimacy of social contact, and the frequency and pattern of those contacts. Intimate contacts entailing exchange of bodily fluids (e.g. nursing, feeding via regurgitation, coprophagy) may influence microbial transmission more strongly than less intimate physical contacts (e.g. manual grooming) or spatial proximity. Moreover, the rate and patterning of those contacts will determine each individual's exposure to the social microbiome. For instance, when group members vary considerably in the number and frequency of social contacts, this may lead to higher between-host heterogeneity in gut microbial diversity. Members with higher centrality within a social network can exert greater influence over the network and typically possess more connections, while socially isolated or more outlying members possess fewer such connections. We hypothesise that the microbiomes of these central individuals will resemble the social microbiome more closely. Individuals may benefit from, or pay costs associated with, exposure to the social microbiome. For instance, if an individual loses beneficial microbes due to illness or antibiotics, they may be recolonised via the social microbiome. Conversely, individuals who are better connected within the social network may also be more exposed to pathogenic microbes and parasites.

Level 2 – Within-Group Processes: Social group size, network modularity, group demography (e.g. sex and age distribution), and the degree of behavioural coordination between group members may all influence the structure and dynamics of the social microbiome and ultimately the composition and function of individual microbiomes.

Group Size: Large groups are characterised by an abundance of hosts (and thus colonisation opportunities). Since any individual microbiome will represent only a small proportion of the total microbial variance, the social microbiome may be more stable and resilient since in larger groups. In smaller groups, changes within individual microbiomes may trigger large and long-lasting alterations in the social microbiome. Hence, the stability of the social microbiome should vary positively with group size. To some extent, these ideas reflect a standard concept from island biogeography theory[29,30]: small islands are likely to diverge down idiosyncratic trajectories because they are sampling a much smaller subset of the available range/taxa and are more sensitive to ecological drift. In the instances where the social microbiome of a large group does show rapid changes, this may indicate the presence of particularly virulent and infectious microbes that are quickly moving through the network, or else microbial blooms due to new (e.g. seasonal) nutritional resources.

Behavioural Coordination: Behavioural coordination among group members may enhance or obscure signatures of the social microbiome, especially in relation to the gut microbiome. Many social animals exhibit behavioural coordination. For instance, troops of baboons travel across the landscape together and consume similar nutrients at similar times and a pride of lions will hunt and eat together from the same kill. Human social groups will often eat meals comprising the same elements at the same time, and in some cases may share beliefs that constrain nutritional choices (e.g. vegetarianism in a family or social community). Such behavioural coordination is likely to amplify gut microbial similarity among group members. This is because consumption of similar meals at similar times may lead to microbial species

sorting in the gut, creating similar microbial communities even in the absence of between-host transmission. Interestingly, behavioural coordination may have different effects on different microbiomes in the same individual. For example, in a recent study of Egyptian fruit bat colonies, researchers found that microbes in the animals' fur exhibited synchronous changes over time, while the gut microbiome did not[102].

Social Network Modularity: The rate and patterning of contacts within a social group may determine the degree of heterogeneity of the social microbiome. For instance, social networks vary in their modularity: some are well mixed, while others are highly clustered with social cliques, such as in chimpanzees, geladas, hamadryas baboons, hyenas, and elephants. All of these species live in fission–fusion societies where individuals form their strongest bonds with a small subgroup, but they also form weaker bonds with other conspecifics, resulting in a modular network. The social microbiome of social groups with modular networks is expected to exhibit greater heterogeneity and lower stability as compared to similarly sized groups that are well mixed.

Sex Distribution: Mammalian social groups vary in the number of adult females per adult male[103]. Because host sex is sometimes an important predictor of microbiome composition[63,104,105], the sex distribution in a social group may influence which microbes are most likely to be transmitted. In some cases, there are no adult males with stable group membership (e.g. elephant herds comprise mostly females, with the only males being juveniles). Males and females often vary in the nature and frequency of their interactions, and where groups differ in their sex ratios, this may lead to differences in the social microbiome. For example, female–female grooming relationships in baboons are more reciprocal than male–female relationships, while male–male grooming interactions are relatively rare[106-108]. If grooming is an important mode of microbial transmission[50], the social microbiomes of female-biased groups might be more homogeneous than groups with relatively more males. In general,

male-biased and male-only groups are less common than female-biased groups and are usually short-lived, though there are numerous instances of such coalitions. A few examples include wandering groups of bachelor gorillas, bison, deer, and recently evicted adolescent lions in search of a new pride.

Age Distribution and Life History Stage: Microbial composition varies across the lifespan[62,104,105], and age also plays an important role in the nature of social interactions within a group. For example, infant mammals receive intensive caregiving from their mothers (e.g. nursing, licking, and grooming). These parenting interactions decline with age, and the developing mammal will acquire new social connections with other group members. Indeed, there is some evidence suggesting that social contact during early development amongst weaned rhesus macaques can rapidly alter microbial composition[84], which supports the idea that non-parental interactions in early life influence the microbiome, in addition to parental interactions. The influence of parental interactions on the microbiome fades as the juvenile primates age and form social bonds with other adults. Reproductive interactions will also increase with the onset of sexual maturity.

Similarly, life history stage may also influence which microbes are transmitted. For instance, research in humans and mice has shown that *Bifidobacterium* is dramatically elevated in the late stages of pregnancy[109,110]. Therefore, we predict that female primates in the late stages of pregnancy may transmit greater levels of *Bifidobacterium* compared to females at other life history stages and males.

Level 3 – Between-group Processes: In terms of network theory, host groups may be considered as modules[111] that are connected to other such modules within a network spanning multiple social microbiomes (i.e. social groups may interact with other social groups of the same species which may result in microbial exchange between their social microbiomes). Although between-group interactions can be affected by some of the same factors as group-

level interactions, the social microbiome may be shaped by between-group interactions in ways that may be readily understood from group-level interactions alone. We therefore describe group-level (Level 2) and between-group (Level 3) processes separately, focusing on territoriality, inter-group aggression, and inter-group dispersal as examples of between-group processes that are expected to affect the extent to which social groups exchange microbes and influence one another's social microbiomes.

Territoriality: Differences in territoriality, especially the degree to which social groups maintain exclusive access and control over a home range, will affect the extent to which neighboring social groups influence the social microbiome of a given group. If a species is highly territorial (e.g. lions, wolves), the social transmission of gut microbes between neighbouring groups should occur largely via migrating conspecifics. However, if different groups have overlapping home ranges (e.g. elephants, baboons), microbes may spread between groups not only through migrating conspecifics, but also via faecal contamination of the physical environment. Since gut microbes differ in their capacities to survive in extra-host environments (e.g. variation in oxygen tolerance), these between-group effects on the social microbiome are likely to be stronger for some microbial taxa than others, influenced by the extent to which they are dependent on their host. Overall, between-group microbial transmission may be greater (resulting in more between-group similarity) amongst animals with overlapping territories, as there will likely be greater incidental contact between groups. Indeed, such a pattern has recently been observed amongst colobus monkeys[88].

In addition, there are cases where microbes contribute to social odours and territorial group identity[112]. For instance, bacterial communities in the scent glands of mammals such as hyenas[113] and meerkats[114] are distinguishable on the basis of social group, and contribute to group-specific social odours. These may in turn characterise the secretions used for scent marking their territories. Moreover, many animals engage in faecal marking across their ranges,

including coyotes[115], wolves[116], ringtails[117], antelope[118], rabbits[119], and rhinoceroses[120]. These faecal markings are thought to act as a form of signalling between conspecifics. Sniffing or otherwise interacting with these faecal markings could facilitate within-group, between-group, and interspecific microbial transmission, particularly for microbes that possess mechanisms to survive extra-host oxygen-rich environments (though it is unlikely that this will be a key mechanism of transmission).

Aggression: Another potential mechanism for between-group microbial transmission is between-group physical aggression, often as a consequence of territoriality. Amongst primates, for example, species vary considerably in typical levels of aggression[121]. Aggression in chimpanzees has been particularly well-studied, and groups of chimpanzees (especially males) are known to attack members of neighbouring troops[122-124]. Lions and lionesses also engage in physical, aggressive confrontations with intruders from other prides[125,126], and wolf packs engage in physical aggression with one another over territory[127]. If direct contact increases rates of microbial transmission between individuals, more aggressive encounters between groups may facilitate the transmission of microbes between groups. However, only a minority of aggressive encounters entail or result in physical conflict. Rather, many aggressive displays are intended to intimidate opponents in order to inhibit engaging in energetically costly physical conflict, and as such there would be no microbial exchange in such non-physical encounters. Overall, given that direct physical aggression is relatively rare, physical conflict is likely to be a weak mechanism for between-group microbial transmission at best.

Dispersal: In adolescence and adulthood, social animals will often leave or be evicted from their natal groups to join established groups or form new groups. These dispersal events have implications for within-group social behaviour and between-group gene flow[128]. Several hypotheses seek to explain immigration and emigration. For instance, migration diminishes the genetic risks of inbreeding, may offer new reproductive opportunities or greater access to

resources for the immigrants, and reduces mating competition for dominant members in the natal group[129-133].

Emigration and immigration will have several implications for the social microbiome of the natal and receiving groups (see Figure 3). Over time, the microbiome profile of the immigrant is expected to reflect the compositional average of the gut microbiomes of members of the new group, weighted by their degree of social contact with the immigrant. Since primate social groups can be distinguished on the basis of their microbiomes[50,55,60,82-84,88,89], and since social contact promotes microbial transmission [50,53,55,77], joining a different social group will likely lead to changes in the microbiomes of both the immigrant and the social group as a whole.

If the number of immigrants is small and the receiving group is large, then immigrant microbial contributions to the new microbial metacommunity are expected to be correspondingly small, whereas changes in the microbial profile of an immigrant are likely to be larger and may be predicted by the composition of the social microbiome. Some support for these predictions derives from a specific investigation of microbial composition in dispersing male baboons[51]. Immigrants to the new group showed gradual changes in microbial composition over several years, increasingly resembling the microbiomes of the group's long-term members. Similar patterns have also been noted in lemurs, with immigrant males developing microbial signatures resembling those of the residents[54]. These results are consistent with the hypothesis that social interactions promote convergence between the immigrant's microbiome and the receiving group's microbial metacommunity.

It is also important to bear the number of immigrants in mind, as a larger number of migrants should, on average, create larger effects on the social microbiome compared to fewer or single migrants. For example, in lions, males (and in some cases, females) will leave their natal prides in groups[133]. Similarly, in meerkats, males and females emigrate from their natal

mobs in groups[134]. Amongst meerkats, dispersing males may join established groups, or form new breeding groups with parties of females. In such instances, the roving coalition will possess its own social microbiome that should bear some resemblance to, but grow increasingly distinct from, the social microbiome of the natal group. The social microbiome of the roving coalition is likely to be influenced by various biological, social, and physical factors (e.g. Figure 2). Depending on the number of emigrating individuals, each individual remaining in the natal group will have a greater influence on the social microbiome since each remaining member now contributes a larger proportion of the total microbial variance.

Finally, the effects of immigration on the social microbiome may also vary as a function of the sex and reproductive status of the roving animals. For instance, in female-biased migration, migrant females may alter the receiving group's social microbiome more strongly compared to males, due to direct mother-to-infant transmission of microbes during birth. On the other hand, if a migrant male is able to monopolise access to a large group of females, then he may exert considerable influence over the group's social microbiome.

The sensitivity of the social microbiome to immigrants also raises questions about whether the immigrant's microbiome modulates their social acceptance within the receiving group. To the best of our knowledge, there are yet no reports of such a phenomenon in mammals. However, studies in ants[135] and termites[136] have found that antibiotic-induced ablation or alteration of microbes could lead to rejection from the colony, suggesting that there are animals in which microbially derived signals contribute to social recognition and acceptance.

Level 4 – Population- and Species-Level Processes: Beyond the features of group living, several other aspects of a species' lifestyle will influence its social microbiome. These include behavioural differences between species such as the degree of sociality and nature of the mating system. Further properties at the population- and species-level include genetic

factors such as the average relatedness within a social group (which varies considerably between species; see Box 2). Lifestyle factors also include abiotic features linked to the host's physical environment (e.g. whether the species is terrestrial or aquatic, arboreal or ground-dwelling; see Box 3). Together, these features are likely to affect the degree to which processes at other levels are enhanced or attenuated by the environment.

Average Sociality of the Species: Animal species vary in the frequency and nature of their social contacts with conspecifics (e.g. tigers have fewer social contacts than lions). At a minimum, many sexually reproducing animals that rely on internal fertilisation will have social interactions during mating encounters, and all mammals form social bonds of some kind, if only between mother and offspring. This variation in sociality between host species will directly affect the number and nature of opportunities for microbial dispersal. Therefore, we hypothesise a positive association between the average sociality of a species and both the frequency of opportunities for inter-host microbial colonisation as well as the similarity and diversity of microbiomes of individuals in a social group (see Box 4 for an in-depth discussion of the relationship between social group characteristics such as size or average sociality and microbial diversity).

Mating Systems: Mating promiscuity may also affect species-level differences in microbiomes. For instance, lion prides are polygynous, comprising a few reproductively active males, some subordinate males, and a larger number of females. On the other hand, meerkat and mole-rat social groups comprise both males and females, with a female at the head of the hierarchy. In contrast to such societies, monogamous mammals that form long-term mating partnerships (e.g. prairie voles, California mice, klipspringer antelope, titi monkeys, and gibbons) may be expected to harbour social microbiomes that are more prone to microbial extinctions due to a paucity of hosts that can serve as microbial reservoirs. However, it should be noted that many monogamous mammals still live in social groups, where some degree of

contact could reduce the likelihood of stochastic microbial extinctions (see Box 4). In contrast, the risk of such microbial extinctions may be highest in mammals such as tigers, which typically form only brief mating partnerships.

Parenting Style: Across many animal taxa, including insects, offspring are directly handled not only by their mothers, but also by other community members, and will inevitably be in close proximity to conspecifics[137-140], all of which could transmit microbes to the infant. In monogamous birds and in mammals for which caregiving is a biparental endeavour, there will also be substantial social contact with the father. In these cases, the father also serves as a reservoir for microbial transmission to the infant. In animal societies with alloparenting, several members of the social group interact with the infant, and these interactions provide opportunities for microbial transmission. In these cases, the infant gut is exposed to a larger subsample of the social microbiome. Thus, whilst infants acquire their initial microbiome during birth[141], subsequent social transmission of microbes, such as in caregiving interactions and interactions with peers may play an important role in shaping the gut microbiome[53,84,143]. Overall, therefore, the infants of species that have paternal parenting and alloparenting are hypothesised to have greater socially mediated microbial diversity compared to species with only maternal care.

Monotocy and Polytocy: Whether animals are monotocous (infants are typically born individually) or polytocous (infants are born into litters of varying size) may also affect early community assembly via microbial transmission from the mother. An infant mammal's initial microbiome is first seeded by the mother during parturition. For instance, vaginally delivered human infants are initially colonised with microbes derived from maternal vaginal and faecal microbial communities. The various microbial communities across the host's body diverge in the first few weeks of life, based on the microenvironments present in different body habitats[144,145]. The initial gut and oral microbial communities are largely dominated by

maternally-derived microbes[144,145,146]. As infants age, other environmentally derived microbes—notably those from family members—colonize the gut[146]. However, evidence from strain-level analysis of the infant microbiome indicates that maternally derived strains of a given microbial species tend to colonise infants in a more stable manner than environmentally derived strains[145], possibly due to the advantage of early introduction to the host. Such findings not only indicate a significant maternal effect on the infant microbiome for at least the first few months of life, but also reveal that the wider social environment can influence the gut microbiome. Nevertheless, this conclusion is based mainly on results from humans, where single births are most common. When animals are born in litters, each infant may act as a microbial reservoir for its siblings, thus helping to maintain the stability and diversity of their microbiota. Therefore, even as exposure to the maternal microbiota declines as infants age and become more independent from their mother, they might still be re-seeded with maternally sourced microbes indirectly through interactions with littermates. Similarly, larger litter sizes would therefore provide more hosts to support a larger effective population of microbes, which is expected to result in a microbial community less prone to the effects of drift (see Box 4). Under this hypothesis, we would predict a positive association between litter size and the duration and strength of the maternal microbiome imprint on the infant gut microbiota.

Level 5 - Microbial Exchanges between Sympatric Species: Some degree of microbial exchange will also routinely occur between sympatric species[147]. Interactions between co-resident species may influence the social microbiome via trophic interactions, symbiotic relationships, and domestication.

Trophic Interactions: An animal's natural diet (e.g. herbivory, carnivory) will have implications for the composition of a social group's microbial metacommunity. Carnivores are likely to be colonised by microbes from their prey, a phenomenon that has been observed in a

wide variety of North American predator–prey relationships[38]. Similarly, chimpanzees that hunt colobine monkeys have some degree of overlap in terms of microbial composition with their prey[60]. Findings such as these point to the idea that microbes flow through predator–prey networks. Thus, a fraction of the microbes constituting the social microbiome of carnivores may be derived from the animals they consume. Plants are also colonised by distinct microbial communities, and plant eaters may be colonised by some of the plant-associated microbes that they consume. For instance, a number of plant-associated bacteria, fungi and viruses were shown to transiently colonise the guts of humans consuming short-term plant-based diets[148].

Symbiosis: Commensal, mutualistic, and parasitic interactions between animals may also facilitate microbial exchange in symbiotic partnerships, with potential subsequent microbial transmission through the social group of each partner. To our knowledge, there is yet no evidence of such microbial transmission between symbiotic partners but this would be an important area to investigate. One possible example, though highly speculative, is the mutualistic interaction between oxpeckers and the large mammals on which they graze for ectoparasites such as ticks, including oxen, buffaloes, zebras, giraffes and impala. Such interspecific interactions provide potential opportunities for novel exposures to – and colonisation by – the microbes of other species.

Other instances of interspecies interactions include mixed flocks of birds[149-151] and mixed herds of mammals[152-154]. Many of these mixed-species groups provide important benefits in terms of reductions in predation risk and improved foraging[155]. One example is the recently described commensal association between geladas and Ethiopian wolves in the Guassa Plateau, in which the grazing baboons improve the wolves' predation success in hunting rodents, and the wolves refrain from opportunistic hunting of young baboons[156]. Since the wolves and baboons feed and reside in the same area, this may provide some opportunities for microbial dispersal between them, particularly through faecal contamination of the

environment. In such cases of mixed-species associations, interactions between species (e.g. via faecal contact or incidental physical contact) may result in increased diversity within individual gut microbiomes. However, given the abundance of factors that can influence the diversity of the gut microbiome, such indirect or weak interactions between different species may have a negligible effect. In comparison, symbiotic relationships that involve direct contact and are long-term (or repeated over time), may exert a stronger effect on the microbial composition of the symbiotic partners, possibly resulting in an increase in diversity within the microbiome of each symbiotic partner, and an increase in the similarity of their respective compositions over time.

Domestication: Humans have long histories of association with numerous mammalian species. Close, continuous interactions with domesticated animals provide opportunities for interspecific microbial dispersal, and may be thought of as a form of symbiosis as well. Domesticated mammals include horses[157], cattle[158], camels[159], pigs[160], sheep[161], and dogs[162], all of which were domesticated by ancient human societies in various parts of the world thousands of years ago.

The dog and human microbiomes are already known to influence one another in modern households[62,65], and it is likely that similar interactions between humans and other domesticated species provide similar channels of microbial dispersal. Indeed, recent research has found that humans, cattle, and semi-captive chimpanzees sharing the same physical environment near Lake Victoria in Africa also share several bacterial taxa, indicating the dispersal of microbes between species and subsequent colonisation of new hosts[163].

In addition to interspecific microbial exchange via interactions with sympatric species, several domesticated animals have played a profound role in shaping our dietary history. In particular, animals such as cows, buffalo, yak, sheep, goats, and camels have all provisioned human communities with milk, which itself contains both microbes and prebiotics in the form

of milk oligosaccharides[2,164]. These too are likely to modulate the microbiomes of human consumers. There are also numerous cultural practices that are likely to facilitate interspecific microbial transmission. For example, it is common in rural India to mould cow dung into 'cakes' with one's hands (once dried, these are used as a fuel source). This practice is likely to result in microbial transmission from cows to humans in these communities.

More generally, researchers have become interested in how domestication can change gut microbial communities of domesticates, and how these changes may resemble the changes induced by shifts to industrialised lifestyles[165]. For example, the gut microbial communities of domesticates may harbour a specific signature of domestication (e.g. domesticates may cluster more closely to one another than they do to their wild progenitors, or they may show less microbial variation, both at the individual and population level, than seen among their wild progenitors). We might also expect greater microbial similarity between humans and domesticated animals compared with between humans and wild progenitors. Finally, selection by humans for rapid growth and efficient reproduction in domesticates may also select for certain bacterial communities and such microbial signatures might be observed across domesticated taxa.

Conclusions

Until recently, research on animal social networks has focussed primarily on the transmission of pathogens and parasites. However, researchers are now beginning to investigate the transmission of mammalian commensal and mutualistic gut microbes via social contact. The transmission of microbes via social interactions is a biobehavioural phenomenon that sets the stage for the analysis of microbial dispersal across mammalian social networks. In this context, we propose that the microbial metacommunity of an animal social group, which we refer to as the social microbiome, should be considered as an important unit of analysis. We outline specific predictions regarding how individual-, intragroup-, intergroup-, intraspecies-

and interspecies-level processes may shape the social microbiome. In addition to considering how factors relating to the host (e.g. its social and physical environment) affect the social microbiome, it will also be important to consider the differential transmission of microbes within the social microbiome, depending on microbial characteristics such as abundance and aerotolerance (see Box 5). Given the important role of the microbiome in animal physiology, the social microbiome therefore has the potential to confer both costs and benefits to individual fitness in ways yet to be studied empirically. Considering microbiomes in the context of social networks, and the emergent microbial metacommunities, provides exciting avenues for a comprehensive understanding of the assembly and impact of microbial communities within hosts.

Boxes

Box 1: Social Transmission of Microbes between Laboratory Animals in Controlled Environments

Co-housing laboratory animals creates shared environments, increasing the probability of direct or indirect contact and enhancing microbial similarity. Genetically similar mice sourced from different vendors are known to vary in gut microbial composition[166-169] and bacterial load[170], which can significantly affect host phenotypes. For instance, segmented filamentous bacteria (SFB) are sometimes present in laboratory mice and their presence confers higher counts of T_H17 cells, increased expression of inflammatory and antimicrobial defence genes, and improved resistance to the pathogen *Citrobacter rodentium*, compared with SFB-free mice[171]. Isogenic mice sourced from different vendors can have differential susceptibility to bacterial pathogens, including *Salmonella enterica* Typhimurium[172] and *Plasmodium yoelii*[173]. This differential susceptibility to disease was partly attributed to variation in the gut microbiota, as gnotobiotic mice colonised via faecal microbial transplants recapitulated the susceptibility profiles of their donors.

Amongst animal researchers, it is now well accepted that interventions targeting the gut microbiome must control for shared environmental exposures to minimize the possibility of misinterpreting environmental signals as treatment effects[174]. These control strategies include cohousing animals prior to the start of interventions, distributing littermates or cagemates symmetrically across treatment and control groups, exposing animals to foreign faecal communities via medium exchange (e.g. bedding for mice, water for fish), controlling for cohousing in statistical analyses, and inter-crossing groups and using F2 littermates (the third generation) in research[174,175]. These strategies are implicitly founded on the idea that social contact among animals within a cage or pool facilitates microbial dispersal, a process that is further enhanced in coprophagic species such as mice[176,177].

Microbial dispersal amongst cohoused animals can be sufficiently strong to overcome gut microbial differences mediated by other factors, such as antibiotic treatment[178,179]. For instance, in a study that stratified mice based on gut microbial enterotypes, mouse strain explained 19% of residual variation whereas cage ID explained 32%[177]. In addition, an experimental study in zebrafish found that gut microbial dispersal across poolmates was sufficient to normalize initial differences in microbiome composition between wild-type and *myd88*$^{-/-}$ immune-deficient hosts[35]. For this reason, cohousing animals is routinely used as a strategy for transferring phenotypes mediated by the gut microbiome, such as susceptibility to metabolic disease[180] or colitis[181], or protection from metabolic syndrome[182].

Nevertheless, whether cohousing is a reliable approach to normalizing the microbiota across an experimental cohort remains unclear. While normalization has been observed after cohousing mice from different litters at weaning[176], other studies have reported the persistence of native microbial communities at some gut loci[174]. In addition, recent studies have reported asymmetries in the extent of microbial sharing among cagemates[166,180]. For example, a study involving the cohousing of gnotobiotic mice colonized from human twins discordant for

obesity found that the lean microbiome would disproportionately invade the obese microbiome under low-fat diet conditions, but this effect was limited under high-fat diet conditions[180]. Finally, other studies have reported that stochastic changes, rather than founder effects, have a greater influence on gut microbial community assembly over time[183]. Such results illustrate that cohousing does not simply produce gut microbial averaging, but rather involves complex interactions between the microbiota, diet, and environment across time. In turn, these interactions are likely also influenced by the degree of social contact among cagemates, even in the context of a controlled experimental space.

Box 2: Species- and Population-Level Genetic Factors

Host social groups vary considerably by species in terms of average intra-group genetic relatedness, and this may have implications for the social transmission of microbes (Level 4). Several studies have suggested that the influence of host genetics on the microbiome is smaller than factors such as diet, medication and the external environment [17,22,184,185]. Nonetheless, studies in both humans and mice have shown that host genes do play some role in shaping the microbiome[18,19,184,186-189]. Furthermore, genetic mutations and manipulations can produce large changes in the microbiome[190-193], supporting the role of host genetics in influencing microbial populations. It should also be kept in mind that the findings that external factors exert substantially larger effects on the microbiome than host genes are based on comparisons *within* species. As more distantly related host lineages are compared, however, the effect of host genetics on the microbiome may be found to be greater.

When considering the social microbiome, it is also important to take into account the effect of genetic relatedness on the development and composition of individual microbiomes within a social group. In particular, greater relatedness between hosts may promote more successful microbial colonisation in new hosts, given a more similar genetic background in the receiving host. On the other hand, individuals that are less closely related to one another may

impose potential genetic filters that in turn pose greater barriers to successful microbial colonisation. Notably, species differ in the average genetic relatedness between group members, and social groups in which breeding opportunities are mostly monopolised by a single dominant individual (e.g. meerkats, mole-rats, monogyne ants, and bees) have higher degrees of average genetic relatedness between members, with more full- and half-siblings.

Notably, the effect of genetic relatedness on the microbiome is not consistent across species. In particular, genetic relatedness has been associated with microbial similarity in mice[187] and in some studies of humans[18,19,188,189,194-196]. However, genetic relatedness was not found to be associated with microbial similarity in nonhuman primates such as chimpanzees[83] and colobus monkeys[87]. This difference in results suggests that genetic effects are likely weak, and therefore only detectable in large samples. However, it is possible that if these analyses were repeated using strain-level metagenomic data, we might observe that genealogy in chimpanzees and other primates plays a role in determining strain-level microbiome composition. Furthermore, a weak association or the absence of associations between genetic relatedness and microbial similarity may be expected in animal social groups characterised by generally lower levels of genetic relatedness (e.g. chimpanzees). Indeed, it may be that kinship is more strongly related to microbial similarity in animals where the average genetic relatedness is an order of magnitude higher (e.g. mole-rats, meerkats, and eusocial insects). Characterising the effects of genetic relatedness on microbial similarity across a wide range of taxa will therefore be an important task in understanding the extent to which host genes structure the microbiome. Of course, it is necessary to control for social interactions in such studies as individuals within a group who are more closely related are also more likely to interact with one another. Thus, it is important to disentangle the relative effects of social interactions versus genetic relatedness on microbiome similarity.

Studies of parasite transmission in eusocial bumble bees has found that close genetic relatedness amongst bumble bees promotes transmission of the parasite *Crithidia bombi*, whilst higher levels of genetic variation provide protection[197,198]. If parasite transmission benefits from genetic relatedness amongst hosts, it may be worth investigating whether bacterial transmission also benefits from host relatedness. We predict that individual microbiomes will be more similar in social groups where genetic relatedness is high. Furthermore, we hypothesise that the social microbiome of a social group characterised by high genetic relatedness might be more stable than that of a social group whose members are less closely related. However, in the event of invasion by high-virulence parasites or pathogens, the genetic relatedness between hosts could contribute to a more rapid spread of infection, which would also likely exert a greater destabilising effect on the social microbiome compared to groups in which the hosts are less related to one another. It is also worth keeping in mind that increased relatedness could be due to paternal or maternal origins, depending on the society under consideration. Increased relatedness in the paternal line (due to a single male) might exert a smaller influence than increased relatedness in the maternal line, due to the additional contribution of vertical transmission of microbes from mothers to infants.

Box 3: Habitat, the Physical Environment, and Seasonality

Abiotic features of the host's lifestyle are also likely regulate the opportunities for microbial transmission (Level 4). These include, for example, the nature of the physical environment the host and its social group inhabit, and the effects that seasonal variation exerts on both host sociality and the availability of nutritional resources.

Habitat and the Physical Environment: Habitat and physical environmental features will likely regulate opportunities for the social transmission of microbes. For example, arboreal species such as howler monkeys[55] show reduced similarities in microbial composition compared to other primate social groups[50,53]. In contrast to terrestrial and semi-arboreal species,

incidental contact with faeces is reduced in completely arboreal animals, and is associated with reduced similarity of microbial composition among group members[54,199]. However, because arboreality and group size are negatively correlated[200,201], it is difficult to differentiate the effect of arboreality from social group size without a larger sample of species. Microbial transmission between social groups may also be impeded by physical geography. For example, both arboreal and terrestrial social groups are likely to be structured by the presence of streams and rivers, which delineate the natural ranges of many mammals[202], and which may therefore affect microbial transmission between social groups as well.

Almost all of our knowledge about the social transmission of microbes in mammalian social groups derives from terrestrial or arboreal animals (mostly primates). Little is known about the social transmission of microbes in other types of environments such as animals living in subterranean societies, including mole voles and mole-rats; animals that inhabit and interact with one another in both aquatic and terrestrial habitats (e.g. hippopotamuses, seals, and walruses); and animals in aquatic environments such as cetaceans, including dolphins[203-205] and killer whales[206-210], who live in complex social groups. A few studies have begun characterising skin, oral, and gut microbial composition in dolphins and whales[211-214], paving the way for research on socially mediated microbial transmission amongst cetaceans. Social transmission of microbes in aquatic environments is highly likely to be associated with different sets of filters and mechanisms compared to terrestrial transmission, and these are yet to be rigorously characterised.

Seasonality: Seasonality may have population-wide consequences for the frequency of social interactions and hence the composition of the social microbiome. Overall, microbial diversity and similarity may be expected to be greater during seasons that promote social interaction. For example, chimpanzees are more sociable in wet compared to dry seasons, and this seasonal change in social behaviour has been linked to higher richness and lower inter-

individual variability in gut microbiomes of individual hosts[53]. Another example of possible seasonal effects on microbial transfer is that savanna-dwelling animals tend to cluster around waterholes during dry seasons, leading to increased opportunities for within-group, between-group, and between-species transmission of microbes.

One challenge will be uncoupling effects of season on sociality from the effects of season on diet, as variations in nutrition across wet and dry seasons will themselves affect microbial composition. For example, there is considerable season-dependent change in the gut bacterial genera of capuchin monkeys, driven by fruit and arthropod availability[215]. Research on Hadza hunter-gatherers in Tanzania has shown that gut microbiomes vary between seasons, based on factors such as diet, with microbial diversity being greater in the dry season compared to the wet season[21].

Box 4: The Relationship between Microbial Diversity and Group Size and Sociability

Studies in chimpanzees[53], pikas[216], sparrows[217], and now in humans[78] have reported positive associations between the degree of host sociality and α-diversity of the gut microbiota. The underlying mechanisms driving associations between the degree of individual sociability and α-diversity within the host gut microbiome remain unclear. Larger group size increases the total number of islands available for microbes, potentially increasing the diversity of the social microbiome, similar to positive associations between habitat area and biodiversity in other systems. This increase in microbial diversity may allow individuals to acquire a greater variety of gut microbes.

However, a parallel and opposing mechanism may also be acting to reduce microbial diversity: larger groups or higher rates of social interaction allow for existence of larger effective populations of microbes within the hosts' microbial metacommunity (the social microbiome). Thus, natural selection may operate more efficiently and can act on even small differences in fitness between microbial strains when the effective population size is large.

All else being equal, population genetic theory predicts that evolution in smaller microbial populations is more likely to be influenced by the effects of genetic drift (i.e. the random sampling of genotypes in each generation), which may prevent or hamper the fixation of variants with marginal fitness advantages (in other words, diversity that is non-adaptive may be maintained in the population)[218]. In contrast, variants with marginal fitness advantages will more easily sweep to fixation in larger effective populations (e.g. due to large group size or higher rates of social interaction between hosts). This could have the effect of *reducing* diversity, as the marginally fitter microbial strain could outcompete other strains in the social microbiome, and would transmit more efficiently in larger groups and amongst individuals with more frequent or intimate social interactions. In this scenario, the association between microbial diversity and group size or sociability may be attenuated or may even become negative due to the fixation of strains with marginal fitness advantages. However, although this mechanism appears theoretically plausible, it is yet to be empirically validated.

The net outcome of these opposing effects on α-diversity (i.e. rescue of stochastic extinctions by proximal microbiomes and increased habitat space increasing α-diversity versus greater efficiency of natural selection leading to the extinction of less fit strains and thereby reducing α-diversity) will ultimately influence the nature of the association between diversity and group size or sociability. In fact, the strength of one process relative to the other will likely depend on a range of environmental variables.

Box 5: Microbial Abundance and Taxon-Dependent Transmission

We have treated the individual microbiome and the social microbiome as a largely uniform construct in terms of its composition. However, it is important to consider the dynamics of abundant and rare microbial species, microbial lifestyle, and also non-bacterial microbes in the microbiome, notably bacteriophages.

Microbial Abundance: An abundant species that makes up, for instance, 1% of the average individual microbiome will likely be much less sensitive to factors such as group size, strength of social interactions or sex distribution compared to rare microbial species that make up, say, only 0.001% of the microbiome of a few individuals. Rare species will likely be more at risk of stochastic extinctions in individual microbiomes, and consequently, more dependent on the presence of proximal hosts for successful transmission. As such, in a social microbiome, rare species may be especially susceptible to stochastic extinctions. The probability of stochastic extinctions is likely to depend in turn on the various processes that may affect the social microbiome, as described in this article (see Figure 2). For instance, rare microbial species are more likely to survive if their hosts engage in more frequent and more intimate social interactions (Level 1), as well as host species that live in larger social groups which provide more opportunities for colonisation (Level 2). Compared to animals that leave their natal groups individually, animals that disperse in coalitions have a greater probability of carrying rare species from one group to another (Level 3). Animals that bear litters (Level 4) will also likely facilitate the survival of rare microbial species, as a single mother has a greater likelihood of transmitting those species to members of the litter. Close interspecific commensal associations, or close relationships with domesticates, are also more likely to enable the movement of rare microbial species between different host species (Level 5). Thus, whilst both common and rare microbes will benefit from inter-host social transmission, the rare microbes should be more critically dependent on these mechanisms for protection against stochastic extinctions (unless of course they possess attributes that enable survival in environments outside the host).

Microbial Lifestyle and Survival Mechanisms: Bacterial species vary in their dispersal capacity[219], and this likely influences which taxa are more easily transmitted via social interactions. In addition to social transmission, microbes that have mechanisms for

extra-host survival (e.g. oxygen tolerance, desiccation tolerance, and sporulation) could be transmitted to new hosts that are temporally or physically distant by virtue of these survival mechanisms (e.g. these microbes might survive in a faecal marking and reach a new host that investigates this marking). For instance, since *Clostridium* species can form spores, we might predict that they are able to reach hosts that are more spatially and temporally distant. In contrast, obligate anaerobes (e.g. *Bacteroides, Fusobacterium, Prevotella, Veillonella*) that do not possess these mechanisms are more dependent on the sociality of their hosts and the presence of proximal hosts.

Bacteriophages: Finally, it is also relevant to consider other members of the microbiome, in addition to bacteria. Notably, bacterial communities are structured by bacteriophages, the viruses that infect them. The possibility that host-associated bacterial communities are affected by the social transmission of bacteriophages is therefore worth considering. Indeed, as may be expected, there is evidence that bacteriophages are vertically transmitted from mother to infant in humans[220]. Transmission between individuals in a household setting has been demonstrated with the bacteriophage φX174, which specifically infects *Escherichia coli*[221]. In this case, phages that target and lyse pathogenic bacteria within the host gut ecosystem might offer additional resilience to infection and reduce the burden on the host's immune system. Indeed, the bacteriophages against *Vibrio cholerae* appear to attain greater virulence during *Vibrio cholerae* infection in the host, becoming more efficient at lysing the bacteria, and thus providing an additional bactericidal barrier against the pathogen[222].

Conversely, bacteriophages against commensal and mutualistic bacteria may underlie susceptibility to, or be associated with, host pathology by allowing the proliferation of potentially pathogenic microbial communities. For instance, children suffering from impaired growth (stunting), which affects globally over a fifth of children under 5 years, have different

gut phage communities compared to non-stunted children[223]. In particular, there is evidence that phages in stunted children may contribute to higher proportions of gut Proteobacteria, a phylum containing a variety of pathogenic bacteria. This may be due to phage-induced depletion of commensal and beneficial bacteria, thereby leaving open ecological niches for Proteobacteria to exploit. Therefore, gut bacterial communities can be shaped by bacteriophage viruses, and studying the social transmission of bacteriophages and other microbial taxa is an important direction for future research.

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Authors' contributions

A.S. developed the general concept and wrote the first draft of the manuscript. K.V.-A.J. substantially edited the content at all stages. S.H. and A.H.M. contributed text and hypotheses to the manuscript throughout its preparation. E.A.A., L.D.S., R.N.C, T.H.C.-B., R.I.M.D., and P.W.J.B contributed revisions, ideas, text, examples. S.H. drafted the figures, with A.S., K.V.-A.J., A.H.M., E.A.A., and R.N.C providing input. All authors approved the final manuscript for submission.

Competing Interests

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