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**Microbiome Interconnectedness throughout Environments with Major Consequences for Healthy People and a Healthy Planet**

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1           **Microbiome interconnectedness throughout environments with major**  
2                           **consequences for healthy people and a healthy planet**

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55 **SUMMARY**

56 Microbiomes have highly important roles for ecosystem functioning and carry out key  
57 functions that support planetary health including nutrient cycling, climate regulation and  
58 water filtration. Microbiomes are also intimately associated with higher organisms such as  
59 humans, other animals, plants and insects and perform crucial roles for the health of their  
60 hosts. Although we are starting to understand that microbiomes in different systems are  
61 interconnected, there is still a poor understanding of microbiome transfer and connectivity. In  
62 this review we show how microbiomes are connected within and transferred between different  
63 environments and discuss the functional consequences of these connections. Microbiome  
64 transfer occurs between and within abiotic (e.g., air, soil, water) and biotic environments, and  
65 can either be mediated through different vectors (e.g., insects or food) or direct interactions.  
66 Such transfer processes may also include the transmission of pathogens or antibiotic  
67 resistance genes. However, here we highlight the fact that microbiome transmission can have  
68 positive effects on planetary and human health, where transmitted microorganisms potentially  
69 providing novel functions may be important for the adaptation of ecosystems.

70 **INTRODUCTION**

71 Microorganisms are (almost) everywhere on our planet and provide critical contributions to  
72 the establishment and functioning of terrestrial, marine, and freshwater environments.  
73 Furthermore, eukaryotes, including plants and animals, are typically associated with complex  
74 microbial communities that are pivotal for health and functioning of their host. These  
75 microbial communities are also referred to as microbiomes, defined as assemblages of  
76 bacteria, archaea, fungi, viruses, protozoans and other microeukaryotes, as well as their  
77 activities in the context of a given (a)biotic habitat (1). Microorganisms drive local and global  
78 elemental cycles on our planet: for example, they determine soil fertility at a local scale, but  
79 also drive and react to changes acting at a global scale such as greenhouse gas emissions,  
80 climate change and climate change mitigation. Microbiomes play an essential role in many  
81 elements of our society, such as the microbiomes associated particularly with the digestive  
82 tract of humans and other animals, in the treatment of domestic, agricultural, and industrial  
83 waste streams, in fermentative food production, and in the biotechnological production of  
84 bulk and fine chemicals (2). Hence, microbiomes occupy and shape the vast array of  
85 ecological niches available in natural and engineered environments. The microbial  
86 composition and functional capacity in many of these environments is a major theme of  
87 current research, often with the goal of understanding the contributions of microbiomes to the  
88 functioning and health of these environments. Although it is widely accepted that  
89 microorganisms are transmitted between ecosystems, microbial connections between  
90 ecosystems have not yet been explored at large scale, at least in part due to fragmentation of  
91 resources (3, 4). Such interconnectivity is now recognized in what has been coined the One  
92 Health approach (5, 6). Nevertheless, to date this approach has almost exclusively focused on  
93 negative aspects of microbial transmission, such as the spread of (zoonotic) pathogens and  
94 antibiotic resistance genes or organisms related to the production of molecules with adverse  
95 activities, such as mycotoxins (7). In contrast, the potential and extent of more positive  
96 aspects of microbial transmission have not been addressed with equal attention. Such  
97 knowledge, however, and particularly quantitative aspects of microbial transmission routes as  
98 well as the conditions that determine these, would be essential for the optimization and/or de  
99 novo design of microbiome-inspired intervention strategies that can allow safer, more  
100 sustainable, and healthier food and feed production (3). To this end, this review will provide  
101 an up-to-date summary of our current understanding of microbial transmission within and  
102 across different environments, including both the supportive and negative aspects of  
103 microbiome transmission and circularity. This analysis is illustrated with examples from the

104 different domains within food production systems and beyond. We conclude with predictions  
105 of the future directions needed to exploit microbiomes to their full potential.

106

## 107 **MICROBIOME TRANSFER AND INTERACTIONS IN ENVIRONMENTAL** 108 **MICROBIOMES**

### 109 **The soil-plant continuum**

110 The soil-plant system represents a continuum of microorganisms, which are able to  
111 survive both in the plant and in the soil environment and may be exchanged between the two.  
112 Because of this close relationship, the type of vegetation, soil management practices or  
113 environmental conditions greatly influence microbiome diversity and composition of soil as  
114 well as of plant-associated microbiomes. This connection has been extensively investigated,  
115 although connectivity over large distances or to environments beyond the soil-plant system is  
116 less well understood.

117 Dispersal of microorganisms or microbiomes may occur locally, within a field or site, as  
118 well as more widely between different environments. Typical dispersal routes in the soil  
119 environment include dispersal from the air above the vegetation, from nearby vegetation and  
120 leaf litter near the soil surface or from litter below the top layer (8). Microbial dispersal may  
121 also occur via pollen or seeds (9). Different dispersal routes transport distinct microbial  
122 communities that differentially influence microbiota composition in the recipient environment  
123 (6). Dispersed microorganisms may establish over the long term or may only exist transiently.  
124 However, even transient invaders may drive microbial community shifts (10).

125 Soils serves as major reservoirs of plant-associated microbiota comprising plant  
126 beneficial, neutral, or pathogenic microorganisms. Particularly prominent is the symbiosis of  
127 plants with mycorrhizal fungi or of legumes with nitrogen-fixing rhizobia. Other beneficial  
128 microorganisms may have direct effects, e.g., by mobilizing and providing important plant  
129 nutrients, alleviating plant stress (such as drought), or by protecting plants from pests and  
130 pathogens through competition, antibiosis, or the production of enzymes or metabolites (11).  
131 Indirect benefits include, for example, the induction of plant responses leading to improved  
132 resistance to pathogens. The soil microbiome, the environmental parameters, as well as the  
133 physiology of plants all determine which microorganisms are transferred to and establish  
134 within and upon plants.

135 Within the plant there are multiple niches enabling the growth of diverse microbial  
136 communities. In roots, for example, a microbial continuum extends from the rhizosphere soil

137 to the rhizoplane and different niches within the endosphere. Microorganisms colonizing the  
138 plant endosphere can comprise obligate or facultative endophytes (12). The latter are often  
139 environmentally derived, utilizing the presence of a compatible plant tissue as an interim  
140 habitat and resource rather than being dependent on it. Thus, depending on the plant species  
141 and genotype, microbial properties, and environmental conditions, different subsets of  
142 rhizosphere microbial communities enter and colonize roots as endophytes (13).

143 A range of formal interactions and opportunistic events enable rhizosphere  
144 microorganisms to reach inner root tissues (14). These include intricate ‘chemical dialogues’  
145 between the plant and compatible microorganisms (e.g., legumes and rhizobia) that lead to  
146 modification of the host and microorganisms, colonization of root hairs and formation of new  
147 organs. Less formally, compatible or opportunistic microbes can enter root systems through  
148 cracks (e.g., when lateral roots form) or by cell wall degradation (13). Once inside the plant,  
149 microorganisms can disseminate to below- and above-ground tissues by colonizing the  
150 apoplast or the vascular system. Overall, a plethora of opportunities exists for members of the  
151 soil microbiome to enter and colonize plant root systems, spread within the plant, and even be  
152 disseminated to new environments and generations of plants by movement of pollen, seed, or  
153 other tissues.

154

### 155 **Plant seeds as vehicles of microbiota transmission**

156 Some endophytes colonize reproductive organs such as flowers, fruits, and seeds (15),  
157 the latter in particular, being increasingly recognized as habitats for functionally important  
158 microorganisms. Microorganisms colonizing seeds and the spermosphere; i.e., the area around  
159 the germinating seed, can improve germination and increase seedling vigor, but also protect  
160 seeds against rotting or the emerging seedling against disease (16, 17, 18). Seed  
161 microorganisms are to a great extent horizontally transferred as many of them derive from the  
162 soil environment (18, 19), where soil microorganisms colonize and then enter roots and then  
163 systemically colonize plant tissues and seeds. In addition, microorganisms from alternative  
164 sources (e.g., insects, air, rain – 20, 21) may colonize reproductive and disseminative plant  
165 organs by using stems, flowers or fruits as entry points (12, 23, 24). The colonization of  
166 pollen grains by microorganisms may result in the subsequent colonization of the ovule and  
167 the seed after pollination (25).

168 The vertical transmission of seed microbiota has been increasingly identified as an  
169 important route for delivering microorganisms to the next generation plants, especially at



170 early vegetation stages. Well-known examples of vertical transmission of plant endophytes  
171 are members of the fungal genus *Epichloë* (*Neotyphodium* for anamorphs) (26). Similarly, the  
172 vertical transmission or microbial inheritance of bacteria has received considerable attention.  
173 Abdelfattah et al. (27) identified two consecutive stages of vertical transmission – from  
174 parents to seeds and from seeds to seedlings. The authors also defined a third stage, i.e., the  
175 phase of seed dormancy, which requires that microorganisms are able to survive the harsh  
176 conditions of limited nutrient and water availability. Vertical transmission of seed  
177 microbiomes has been demonstrated in many different plant species including maize, rice,  
178 wheat, barley, sugarcane, soybean, tomato, and oak as well as in model plants (9, 19, 20, 28,  
179 29, 30). A survey of seed microbiomes and their transmission routes in several monocot and  
180 dicot plant species showed that the bacterial family *Enterobacteriaceae*, particularly members  
181 of the genera *Pantoea*, *Enterobacter*, *Klebsiella*, and *Massilia*, are vertically transmitted (19).  
182 However, it was shown that pathogenic *E. coli* was not able to penetrate seed embryonic  
183 tissue, neither via the parental vascular tissue, nor via the flower receptacle (31). Among  
184 fungal endophytes, non-pathogenic *Fusarium* and *Alternaria* were commonly vertically  
185 transmitted. Seeds may be widely dispersed (e.g., by wind, water, or animals) in nature and  
186 are much more widely disseminated in the frame of agricultural systems going hand in hand  
187 with a wide dissemination of seed-borne microbiomes.

188

### 189 **The plant phyllosphere and exchange of airborne microbiota**

190 The phyllosphere refers to the plant leaf as a microbiome habitat. The phyllosphere is an  
191 open system which is exposed to, and thereby connected with, the surrounding environment  
192 (32). As such, microbial immigration to the phyllosphere can originate from multiple sources,  
193 both local and remote. Importantly, arrival of microorganisms from the surrounding  
194 environment potentially represents a constant flow of new microorganisms (33), where areas  
195 such as agricultural and horticultural land, forests, grasslands and even urban environments  
196 are sources of microbial inocula (34, 35). Overall, the phyllosphere community composition is  
197 therefore the outcome of multiple factors such as host-based selection, priority effects, natural  
198 successional processes, and stochastic influences (36). Given its exposure to the environment,  
199 the composition of the phyllosphere may be in a constant state of flux.

200 While environmental sources of phyllosphere microbiomes can be diverse, two are of  
201 particular importance: (1) the local vegetation, including both living plants and decomposing  
202 plant material such as leaf-litter or fallen wood, and (2) the soil. Movement of the microbiome

203 from these sources to the phyllosphere can occur via direct physical interactions, for example,  
204 movement and contact of leaves across the surfaces of adjacent plants (37), or via  
205 transmission vectors such as invertebrates or other animals. However, air transport is often the  
206 primary mechanism for movement of material from neighboring environments to the  
207 phyllosphere, particularly when wind combined with mechanical disturbances drive  
208 microorganisms into the atmosphere (38, 39).

209 The efficiency and randomness of airborne transport provide an effective way for  
210 dispersal and exchange of plant-associated microbiomes. This has been well characterized for  
211 foliar plant pathogens (33, 39). Indeed, movement of microbiome members from plant  
212 surfaces into the air, and then transport within the air column, is an effective means to  
213 overcoming geographic barriers. Bacteria, because of their small size, may have extended  
214 atmospheric residence times and, thereby, have potential for long distance transport (see  
215 below). However, bacterial cells are often clumped, and/or attached to plant fragments such as  
216 leaf material. While this is anticipated to protect their viability during transport, it also limits  
217 potential dispersive capability (40).

218 Water droplets are important for microbial transport into and subsequent survival within  
219 the atmosphere. Using population genomics, Monteil et al. (41) demonstrated that  
220 *Pseudomonas* sp. strains pathogenic to cantaloupe plants could be identified within the  
221 atmospheric water cycle (e.g., rain and snow). Similarly, rain has also been shown to be a key  
222 reservoir of phyllosphere microbiota for other plant species (e.g., tomato) (42).

223 It is increasingly apparent there is a reciprocal connection between the phyllobiome and  
224 the atmospheric microbiome, driven by atmospheric processes occurring at global scale. The  
225 phyllosphere is theoretically immense: globally, plant leaf surface area (adaxial and abaxial)  
226 is estimated between  $2 \times 10^8$  and  $1 \times 10^9$  km<sup>2</sup> (43). For perspective, this is up to twice the  
227 Earth's entire surface area. On these leaves, and directly exposed to the atmosphere, some  
228  $10^{24}$  to  $10^{26}$  microbial cells are thought to be present (33) and therefore potentially accessible  
229 to atmospheric transport.

230 Understanding the microbiomes of these environments and the processes that affect  
231 reciprocal exchange, assembly and function of these microbiomes, is critical to understanding  
232 plant health and agriculture. Indeed, it is time to consider these compartments – the  
233 microbiome of the plant (and other terrestrial or aquatic organisms) and the atmosphere – as a  
234 singular holobiome, where especially the plants, microorganisms and the atmosphere have co-  
235 evolved and are therefore to some extent interdependent.

236

### 237 **Air-borne transport of microorganisms**

238       Microorganisms are transported long distances by aeolian (wind) processes (44, 45).  
239 Transport can be as autonomous bodies such as fungal spores, as cells adsorbed to the  
240 external and internal surfaces of mineral particles (dust), or in liquid microbodies (aerosols)  
241 (46). Both the extent of transport and the distance transported are likely to be affected by both  
242 the particle size of the dust, and cell body size of the microorganism (47). Dust plumes  
243 generated from farmlands, drylands and deserts can transport microorganisms hundreds or  
244 thousands of kilometers from their emissive source (44). Dust can rise to very high altitudes  
245 within the Earth's troposphere (as high as 38 km above sea-level) and persist in the  
246 atmosphere for long periods (48).

247       The air masses of the Earth impose some constraints on long distance aeolian transport.  
248 The major tropospheric air masses circulate in the northern and southern hemispheres, with  
249 limited mixing at the equatorial boundary (49). This barrier might limit transfer of particulate  
250 material, aerosols, and microbial cells between the two hemispheres (50). Another barrier is  
251 the limited vertical mixing above the troposphere due to thermal inversion (51). Similarly, the  
252 westerly airflows over the Southern Ocean probably limit transfer of aerial particulates from  
253 the lower latitudes of the southern hemisphere to the Antarctic continent.

254       While the process of aeolian dissemination and deposition of microorganisms is  
255 recognized (52), the ecological consequences of these processes are still being determined.  
256 Microbial activities in the atmosphere impact cloud formation, hydrologic cycles (53),  
257 atmospheric chemistry and processes integral to climate regulation (54). Cloud condensation  
258 and ice nucleation, for example, are common traits across a range of bacteria, fungi, and other  
259 microorganisms, particularly those associated with plants (55). Furthermore, there is evidence  
260 that plant, animal and human pathogens are present in long-distance aeolian transported  
261 microbiomes (56, 57). These also might be associated with disease outbreaks (58). For  
262 instance, a recent study by Björnham et al. (57) showed that the foot-and-mouth disease virus  
263 could be transmitted over distances of up to 50 km. Dust-associated microbiomes harboring  
264 diverse antibiotic resistance genes have also been detected downwind (c.f. upwind) of cattle  
265 feed yards (albeit from near-surface sampling) (59). Human pathogen signals have also been  
266 detected in aerial microbiomes (56). These include the presence of e.g., *Neisseria*  
267 *meningitides* in Saharan dust (60), which was associated with an outbreak of meningococcal  
268 meningitis in Barcelona (61).

269 Fungal taxa are prevalent in the atmosphere due to their resilience and ease of airborne  
270 (spore and conidia) transmission, and several fungal pathogens have been detected in  
271 atmosphere microbiomes. This includes plant pathogens such as *Blumeria graminis* (corn  
272 mildew disease) and *Sclerotinia sclerotiorum* (white mold) (62, 63). Fungal allergens such as  
273 those found in species of *Aspergillus* and *Alternaria* have also been detected at high  
274 concentrations in dust (64, 65), and the presence of these has been linked to increased risk of  
275 respiratory diseases (e.g., 66). Despite these reports on the transfer of pathogens, there is little  
276 understanding on the transfer of non-pathogenic microorganisms via aeolian transport but this  
277 is very likely to occur. Phyllosphere inhabitants including plant beneficial microorganisms  
278 may be lifted into the atmosphere and transported over long distances and return to  
279 phyllosphere habitats. Overall, aeolian transport may mediate long-distance transfer of  
280 microbiomes with potential impact on weather, as well as plant, animal, and human health.

281

## 282 **Insects and microorganism transmission**

283 Hundreds of microbial symbioses are known to exist with insects. Many of those are  
284 ancient, extending back 30 – 250 million years (67). Given the time for co-evolution, it is not  
285 surprising that the symbionts span a range of different relationships, from transient pathogens  
286 to obligate, highly specialized mutualists (68). Microorganisms play diverse and unexpected  
287 roles in the functioning and life of insects such as allowing host diet specialization (69),  
288 provision of specific nutrients or detoxification of chemicals (70, 71), as well as enhancing  
289 resistance to pathogens and parasitoids (72 and references therein). Generally, given the  
290 diversity of insects and the importance of microbial endosymbionts in conferring many traits  
291 and impacting their fitness (72), we have not yet even begun to realize the full extent of  
292 microbiome symbiosis among insects.

293 Many microbial symbionts, especially those colonizing reproductive organs, are  
294 inherited via vertical transmission. These are also termed primary endosymbionts. Vertical  
295 transmission via eggs is common in endosymbionts such as *Wolbachia* spp., *Rickettsia* spp.,  
296 *Spiroplasma* spp., *Buchnera* spp., certain yeast-like symbionts, protists, and viruses (68).  
297 There is increasing interest in understanding the role of microbial-microbial interactions in  
298 vertical transmission. For instance, the type of hereditary microorganisms positioning  
299 themselves first in the next generation of offspring may influence community assembly and  
300 composition (priority effects) of other microorganisms, thereby influencing offspring health  
301 and evolutionary fitness (68, 73).

302 Secondary endosymbionts are often facultative symbionts. These may be transmitted  
303 vertically as well as horizontally (e.g., 74). They colonize different tissues and organs of their  
304 hosts, such as the gut system, muscles or the hemocoel, and usually show lower abundances  
305 than primary endosymbionts. Primary endosymbionts are highly adapted to their hosts,  
306 whereas secondary endosymbionts may be transferred intra- and interspecifically (75).  
307 Horizontal transmission of endosymbionts has been postulated to provide direct fitness effects  
308 to the insect host (reviewed by 72). An additional form is social transmission, i.e., via  
309 transmission between colony mates (76) and sexual partners (77).

310 Insects and other invertebrates represent important vectors of plant pathogens, including  
311 bacteria, fungi, protists and viruses. The importance of insect vectors in transmission of  
312 numerous phytopathogens is well understood (78). However, insects may also transmit  
313 mutualists or entire microbial communities. Lòpez-Fernàndez et al. (22), for example,  
314 demonstrated that the American sap-feeding leafhopper *Scaphoideus titanus* mediated the  
315 transfer of entire plant endophytic bacterial communities between grapevine plants. At the  
316 same time, the endophyte communities influenced the leafhopper's microbiome (22). Such  
317 transfer events can have implications for plant fitness and performance. Furthermore, plants  
318 shape the soil microbiome and insects feeding on plants which are grown on these differently  
319 conditioned soils respond to these changes (79). Hannula et al. (80) performed a study with  
320 herbivorous caterpillars fed on dandelion leaves and showed that the soil microbiome was  
321 partly transferred to the feeding insects.

322 Herbivore-associated bacteria have been reported to suppress plant defenses. For  
323 instance, the Colorado potato beetle secretes symbiotic bacteria capable of manipulating plant  
324 defense responses. These microorganisms elicit salicylic acid-regulated defense, which  
325 counteracts jasmonate signaling. This disruption makes plants unable to fully activate their  
326 jasmonate-mediated resistance against the herbivore (81). Furthermore, different volatile  
327 organic compounds emitted by microorganisms may affect insect behavior. For instance,  
328 *Fusarium proliferatum*, *F. poae* and *F. culmorum* can attract *Tenebrio molitor* larvae, whereas  
329 *F. avenaceum* can repel the same insect (82). Another study showed, that variations in  
330 chlorosis caused by Russian wheat aphid (*Diuraphis noxia*) feeding are determined, in part,  
331 by aphid-associated bacteria (83).

332 Many angiosperm plant species are visited by honeybees (*Apis mellifera* L.) which  
333 collect nectar from flowers. While feeding, the external surface of bees contacts the nectar,  
334 allowing microbial exchange between the bee and nectar. Similarly, microorganisms in the

nectar may be ingested by bees (84, 85). Altogether, these findings suggest that flowers may act as key hot spots for microbial exchange including horizontal gene transfer (HGT) events. Different insects visiting a flower may all receive similar microbiomes. For example, Manirajan et al. (86) found a *Lactobacillus* species in flowers as well as in adults and larvae of seven megachilid bee species. Furthermore, pollen microbiomes of insect-pollinated plant species were found to be more similar than those of wind-pollinated plants. This indicates that insects and the transmission of microorganisms play an important role for pollen-associated microbiomes and a single flower may be involved in a series of transmission events.

Despite high sugar content and osmotic pressure, a range of microorganisms such as yeasts, yeast-like fungi, filamentous fungi and bacteria are found in nectar (84, 87). This ‘nectar microbiome’ has been shown to be functional, modifying sugar and amino acids content (88), and impacting volatile release (89). This is important, as different nectar properties can impact attractiveness of a given flower to pollinators, thus affecting the plants’ success. Indeed, alteration of the nectar microbiome may impact visitation frequency of insects (90) and reproductive success of the plant.

Fungal growing termites (containing the fungus *Termitomyces*) and leaf cutting ants (containing the fungus *Leucoagaricus*) collect plant materials, respectively dry straw, and green leaves, and bring it to their subterranean nests (91) where it is used as substrate for a mutualistic basidiomycetous fungal colony. In return, the termites and the leaf-cutting ants harvest specialized fungal structures, rich in protein and sugars, and use these as feed for their larvae. This unique biomass converting system has been intensely studied, a strong interconnectedness between the microbiomes of the plant materials, the subterranean fungal colony, and the insect has been observed.

We have provided only a few of the many known examples of insect-microbiome transmissions. Nevertheless, they demonstrate the fundamental importance of microbiomes to insects, and how co-evolutionary processes between insects and their microbiomes are not only important for the animal host, but also other components of the ecosystem such as plants. Indeed, it is clear, that the connection of the microbiomes across these systems can influence critical outcomes that affect pollinator and plant success, and thereby ecosystem functioning.

364

### 365 **Microbiome interconnectedness in aquatic environments**

366 Microorganisms are discharged as spray aerosols over water bodies (e.g., sea, lakes, and  
367 rivers). These are produced at the surface of water bodies by wind or transported into the

368 atmosphere over long-range distances. Certain taxa such as *Actinobacteria*, certain  
369 *Gammaproteobacteria*, and lipid-enveloped viruses show high transfer rates to sea sprays,  
370 whereas *Flavobacteriia* and some *Alphaproteobacteria* are transferred less frequently (92).  
371 Understanding the role of marine and other water bodies as a source and sink of  
372 microorganisms and the transfer of airborne bacteria could deliver important understanding of  
373 microbial diversity, spatial distribution, and the interaction between aquatic and terrestrial  
374 microbiomes. A survey on the genetic diversity of airborne and ocean-surface bacterial  
375 communities across the northwest Pacific and subtropical north Atlantic showed that 3% of all  
376 taxa identified were shared between both oceans (93). This study also showed that the  
377 atmospheric microbial community composition over the Atlantic Ocean was dominated by  
378 terrestrial, typically dust-associated microorganisms.

379 The ocean environment harbors microbiomes that have evolved and adapted through  
380 convergent evolution. Coral reef ecosystems are highly productive and diversified marine  
381 habitats that have photosynthetic and primary production features in common with terrestrial  
382 ecosystems. The coral itself is a holobiont and represents a well-recognized model system for  
383 symbiosis. In particular, recruiting or shuffling stress-tolerant microbial symbionts in corals  
384 are important for the recovery from stress events (e.g., coral-reef bleaching) (94). These  
385 ‘symbiosis shuffles’ can also alter the metabolic repertoire of the coral at large (95).  
386 Similarly, sponges are filter-feeding animals hosting extensive microbial assemblages, where  
387 the microbial component may represent up to 35% of the sponge biomass (96). Most sponge-  
388 associated fungi are likely to be sourced from the surrounding environment and belong to the  
389 genera of terrestrial fungi adapted to the marine ecosystem (97). Comparative genome  
390 analysis of *Actinobacteria* associated with a marine sponge showed genomic signatures of  
391 environmental niche adaptation, indicating both terrestrial affiliation and sponge niche  
392 adaptation (98).

393 The coastal marsh soil microbiome sits at the interface of the terrestrial and marine  
394 ecosystems. Both ecosystems host a wide range of microorganisms involved in critical  
395 biogeochemical cycles. At this interface, sea level rise is a threat potentially leading to the  
396 loss of marshes and their associated microbiomes. For instance, increased salinity due to a  
397 rising sea level could negatively impact the microbial metabolism of organic matter by  
398 suppressing carbon cycling genes and their metabolites (99). Salt marshes, which are located  
399 at intertidal wetlands in temperate zones, are one of the marine-terrestrial transition zones for  
400 microorganisms.

401

402 **Transmission of human pathogens and antimicrobial resistance genes in agricultural**  
403 **production systems**

404 The agricultural ecosystem is a congruence, where microbiomes from soil, plants, and  
405 livestock (including manure) come together. Often these systems also include microbiomes  
406 originating from irrigation water, wildlife, wastewater, food chains (e.g., waste and residues  
407 fed to livestock) and humans. How the microbial communities from these different sources  
408 amalgamate in agricultural production systems has consequences for food and feed  
409 production, as well as the health of humans, livestock, and wild animals. The focus here is on  
410 the transmission of food-borne pathogens and antimicrobial resistance.

411 Human pathogens can be present in animal manure and other products of animal  
412 origin used for soil fertilization in some countries. They can be transmitted from irrigation  
413 water or airborne propagules, including open water bodies (e.g., surface water, collected  
414 rainwater) that stay in contact with wildlife such as migratory birds, or which are mixed with  
415 agricultural run-off water or sewage effluent after episodes of severe rainfall (100). Crops that  
416 are consumed fresh, especially those that are harvested after short production cycles, are of  
417 greatest concern for transmission of pathogens to humans. The most commonly observed  
418 pathogens in products of plant origin (e.g., vegetables, fruits, herbs, spices and nuts) are  
419 zoonotic pathogens; e.g., pathogenic *E. coli* strains, *Salmonella* Typhimurium, *Campylobacter*  
420 *jejuni* and *Listeria monocytogenes*. These species prevail in the plant environment (101), and  
421 it is now generally accepted that plants serve as secondary habitats for these zoonotic species  
422 (102). The persistence of human pathogens within plant systems raises concerns for the  
423 emergence of new and possibly more virulent or resistant lines. The rhizosphere is considered  
424 as a hotspot for HGT and when microorganisms from different sources accumulate in this  
425 environment, new traits making human pathogens better adapted to selective circumstances  
426 that prevail in primary food production systems may develop (103).

427 A serious food-borne disease outbreak related to consumption of a plant-derived  
428 product with a huge impact from human and economic perspectives, occurred in Hamburg in  
429 2011. This outbreak was caused by an unusual enterohemorrhagic *E. coli* O104:H4 (EHEC)  
430 type that was presumably present on, or inside fenugreek seeds used for sprout production.  
431 The origin of the outbreak strain was human and not zoonotic, indicating that contact must  
432 have taken place between the fenugreek seeds and sewage either at the production site or at  
433 seed storage or transport locations. From genomic studies it became clear that this strain must



434 have acquired new traits via HGT making it more aggressive but also more resistant to  
435 particular antibiotic classes (104).

436         Large foodborne disease outbreaks related to consumption of plant-derived products  
437 are rare in comparison to outbreaks associated with consumption of animal products, but the  
438 impact of such outbreaks can be significant. Microbiome interconnectivity within primary  
439 food production pipelines is therefore critical in understanding the consequences of mixing  
440 microorganisms from different ecosystems in relation to food safety. Similarly, it is important  
441 for human and animal health to understand how antimicrobial resistant microorganisms are  
442 transmitted via food or feed to our microbiome. Food safety and health aspects related to  
443 microbiome interconnectivity should therefore be taken into account in existing (intensive)  
444 agro-production systems, and particularly in more extensive systems that receive inputs from  
445 side-stream materials obtained from other production systems.

446         Contamination of soils with antibiotics and antibiotic resistance genes (AMR genes) is a  
447 global health concern. Soil contamination is mostly due to the utilization of animal manure  
448 (105) or contaminated water used for irrigation (106). Recent surveys documented the role of  
449 HGT in movement of AMR genes from and among microbiomes in soil to plant tissues (107,  
450 108). Agricultural management practices such as fertilizer application favored HGT. Plant  
451 microbiomes may also host microorganisms resistant to antibiotics and may serve as a  
452 gateway for the transfer of AMR to human or animal microbiomes (109, 110, 111, 112).

453         Livestock and livestock production are also important sources and zones of AMR genes  
454 and HGT, with rumen and gut microbiomes being hotspots for HGT. Comparisons of  
455 microbiomes and antimicrobial resistance patterns in animals have revealed a higher  
456 abundance and diversity of AMR genes in intensive farming compared to extensive farming  
457 (113). In particular, antibiotic administration to animals during intensive farming exerts a  
458 strong selection pressure leading to the enrichment of AMR in agricultural systems (114).  
459 Enrichment of AMR genes within the food chain, especially when these genes are located on  
460 mobile genetic elements (MGEs), is a significant risk for a downstream transfer into the food  
461 chain. Even within foods such as fermented meat and dairy products, horizontal transfer of  
462 genomic elements (e.g., via bacteriophages; 115) can further induce exchange of AMR genes  
463 within dietary microbiomes. Given the importance of food microbiomes in human health, a  
464 more holistic understanding of the exchange of pathogens and AMR genes from the  
465 environment to plants, animals, food, livestock, and human populations is needed.

466

## 467 **FOOD DERIVED MICROBIOTA AND THE HUMAN (GUT) MICROBIOME**

### 468 **The edible microbiome**

469 Plant microorganisms, particularly endophytes, are a fundamental component of human  
470 diets and animal feed. In human diets, fresh vegetables are often eaten raw and contain  
471 different microbiomes: reflecting the plant species and its origin (116). Fresh vegetables and  
472 fruits are therefore an important route for the introduction of microorganisms in the gut (117-  
473 119). For instance, Wassermann et al. (118) calculated that approximately 100 million  
474 bacterial cells are consumed with each apple. However, post-harvest of fruit can dramatically  
475 change the number, types and type of microorganisms ingested (118, 120). Even after  
476 processing (e.g., air-drying, boiling, or preparing a puree), about one third of the original  
477 microbial load was maintained, but with a substantial compositional shift (e.g., higher  
478 abundances of *Pseudomonas* spp. and *Ralstonia* spp., and lower abundances of *Bacillus* spp.  
479 (121).

480 There is a growing body of evidence indicating that both the soil and plant microbiomes  
481 may influence the flavor of food products (e.g., 122). Winemakers have long known that the  
482 soil is central to the physiology of the grapevine and the production of flavor compounds in  
483 the wine itself. Grapes of the same variety grown in different regions (122) have different  
484 metabolic and flavor profiles. The famous *terroir* of the wine has a microbiome element that  
485 extends from the soil microbiome, through direct and indirect impacts on vine physiology and  
486 health, to microbiomes in and on grapes that impact their metabolome during growth and into  
487 fermentation (123, 124).

488 Microorganisms ingested from plants can at least transiently colonize the human gut but  
489 this largely depend on their ability to survive stress conditions of the gastrointestinal tract  
490 (125), although it is not yet clear how food microorganisms interact with and influence the  
491 human gut microbiome (126). The processes of transfer and persistence of microorganisms in  
492 the food system have generally not been explored in depth, and current studies are mostly  
493 limited to pathogens (reviewed by 127) or probiotics (128). Food-associated fermentative  
494 bacteria, including probiotics, may temporarily complement resident microbial communities,  
495 thus forming part of our transient microbiome (128). The application of longitudinal multi-  
496 omics approaches, including high throughput cultivation, confirmed the hypothesis that  
497 bacteria (in particular bifidobacteria) of Parmesan cheese possess the ability to colonize and  
498 persist in the human gut (129). More studies of this nature are required if our fundamental  
499 understanding of the links between food ingested and the gut microbiome is to progress.

500 Along with bacteria, fungi are ingested from food and are transferred to, and interact  
501 with, the gut microbiome. As a part of the gut mycobiota, the genera *Penicillium*, *Aspergillus*  
502 and *Saccharomyces* are typically ingested with plant-based foods (130), *Yarrowia* with  
503 fermented meats (131), and *Kluyveromyces* with dairy products (132). Complex relationships  
504 between gastrointestinal bacteria and fungi from food origins have been reported in humans.  
505 For example, the co-occurrence of pathogenic fungi and inflammatory bacteria and of  
506 potentially anti-inflammatory fungi and bacteria clearly showed how the different components  
507 of the mycobiota interacted and suggested that these organisms may impact the inflammatory  
508 process in the human gut (133). These findings demonstrate the importance of a wider view of  
509 the microbiome rather than focusing on bacteria only. More studies bringing together  
510 prokaryotes, fungi, protozoa and viral components of the entire microbiome, and addressing  
511 how these interact and impact the host gut system, are required.

512

### 513 **Microorganism transfer at the interface between environments and foods of animal** 514 **origin**

515 The transfer of microorganisms from the environment to food of animal origin  
516 (including fish) is an important factor for the understanding and prevention of food spoilage.  
517 While fresh meat and fish products harbor bacterial communities from the gut and skin of  
518 animals as well as from food processing, they also host a core microbiome often derived from  
519 the environment (134). For example, cod and salmon meat samples were shown to contain  
520 different core microbiota, with cod containing more bacteria from seawater than salmon. In  
521 cod, an uncharacterized taxon of *Fusobacteria* was identified, which was also found as a  
522 dominant taxon in the spoiled cod fillet (134). Overall, the transfer of microbiota from the  
523 environment at the initial stages of production of foodstuffs of animal or (plant) origin is not  
524 the result of a simple “contamination” but of microbiome exchange in the environment.

525 The connection between microbiomes within the dairy production/processing chain has  
526 been widely investigated. This has, for example, included tracing origins of microorganisms  
527 present in raw milk. One such study highlighted differences in the raw milk microbiomes in  
528 connection to production systems, comparing those with stock predominantly located indoors  
529 (winter) or outdoors. Regardless of these systems, the teat surface and, to a lesser extent, feces  
530 were identified as the primary sources of raw milk microorganisms (135). Consumption of  
531 raw milk has the potential to expose the consumers to many food pathogens and is generally  
532 not recommended. Much of the world’s milk production is processed before consumption or

533 production of other dairy products, but its microbiome can, in some circumstances, have a  
534 major influence on the final dairy product. In some cases, the microbiomes found within the  
535 processing facility can also have a considerable influence (136). Overall, these studies  
536 indicate the important link between environmental and animal microbiomes influencing food  
537 safety and food production processes, ultimately all determining food quality and nutritional  
538 value.

539

#### 540 **Microbiome exchange in the food/feed (production) environment**

541 The food microbiome derives from the interaction of microorganisms from primary  
542 production, raw materials, operators, environment and production systems (137). While these  
543 microorganisms may be present at a low relative abundance in the environment, their levels  
544 and contribution to food and feed safety and quality can be considerable. These relationships  
545 between different types of microorganisms can be illustrated by the fermentation process,  
546 which is one of the oldest forms of food processing, where fermented foods are a natural  
547 reservoir of complex microbiomes. Fermentation processes involve interactions between  
548 different types of microorganisms as well as multiple metabolic reactions, including food  
549 biomass conversion. The specific role of microorganisms present in fermented foods in  
550 human health is not always clearly evidenced. The fact that many of these microorganisms are  
551 lactic acid bacteria (LAB), and are related to probiotic strains, suggests that at least some  
552 confer health benefits (138). Indeed, a study of the overlap between LAB strains found in  
553 fermented food and human gut (via fecal sampling) microbiomes has highlighted that closely  
554 related strains occur in both food and gut environments, providing evidence that fermented  
555 foods can be indeed regarded as a possible source of LAB for the gut microbiome (126). LAB  
556 in fermented foods are not exempt from the risk of transfer of AMR genes, as evidenced by  
557 microbial transfer events and pointed out as concern by the European Food Safety Agency  
558 (139).

559 Many types of microorganisms can be exchanged in the food-producing environment.  
560 Fungi, protozoa, bacteria, and viruses can all be transferred in food systems; e.g., from  
561 humans (140), materials (141), animals and plants (142) as well as soil and water. In some  
562 cases, their transfer can change the microbial diversity of food ingredients, potentially  
563 contributing to fermentation characteristics and/or modifying the sensorial characteristics of a  
564 food product (143). However, most research has focused on the risk of transfer of pathogens.  
565 For example, transfer of food-borne pathogens from contaminated hands to food represents a

566 potential risk to human health (144). Similarly, human pathogens can be transferred from  
567 animal sources to humans via poor hygiene of food handlers or contaminated equipment  
568 (145). As such, food service establishments are frequent places of microorganism transfer  
569 (146).

570 Microbiomes of built environments, from stable walls, floors, and instrument surfaces  
571 are a key source of inoculum to food/feed production. Particularly in industrial meat  
572 production facilities, the built environment provides both, a contact source for exchange of  
573 microbiomes to foods, also a route for inocula. For instance, in a production facility housing  
574 pigs with unhealthy gut systems and attendant diarrhea, treatment by changing feed alone is  
575 inefficient. However, when the animals are initially treated with pro- and prebiotics,  
576 accompanied by a change in the feeding regime (containing more gut health-promoting feed),  
577 improvements in livestock health can be realized (147). Such practices can result in a stronger  
578 and more resilient piglet health and less reliance on antibiotics, hereby also lowering risk of  
579 antimicrobial resistance (147).

580 Exchange of microorganisms and ARM genes can also involve sources such as silage,  
581 which is often used to enhance the storage stability of animal fodder. However, this feed  
582 source may also facilitate the transfer of microorganisms from the plant microbiome to the  
583 animal gut. Most silage is produced by a conversion of the animal feed carried out by the  
584 microbiome already present in and on the harvested plant materials (viz a mixed culture, via  
585 anaerobic fermentation). Silage conditions favor specific types of bacteria, e.g., different  
586 types of LAB, potentially contributing to a more diverse animal gut microbiome (148).  
587 Finally, it is well known that food microbiomes can also be a hotspot of MGEs including  
588 ARM genes. These microbiomes can be readily exchanged between environments, operators,  
589 among foods, and finally to consumers (149). The processing systems of meat and in  
590 particular fermented meat are considered one of the main sources of ARM genes (150).

591 Microbial exchange in the feed/food production environment has been mostly  
592 investigated in light of food safety and potential contamination with pathogens and/or AMR.  
593 Nevertheless, there is also exchange of non-pathogenic and potentially beneficial  
594 microorganisms, such as e.g., in fermentation processes, playing a role for the production  
595 process itself, but also for providing unique features like taste or nutritional value.

596

597 **Vertical transmission and breast feeding as driver for microbiome development at early**  
598 **stages of life**

599 The human gut hosts diverse microbial communities which are subject to  
600 microorganism exchange between humans. Already at birth, about 50% of the infant's gut  
601 microorganisms originate from the mother's gut, vagina, or skin. Within just 2-5 days after  
602 birth, mother and infant microbiomes can have up to 72% of shared species (151).

603 During and after birth, an infant is exposed to maternal vaginal, fecal, and skin  
604 microbes, and exposure depends on the mode of birth. However, vaginal and skin  
605 microorganisms are usually only transiently found in infant fecal samples, whereas the infant  
606 gut is permanently colonized by gut bacteria that are partly of maternal origin (152).  
607 Predominantly, *Bifidobacterium* spp. and *Bacteroides* spp. are transferred from mother to  
608 child (153): both taxa have the ability to utilize human milk oligosaccharides (154). Due to  
609 their oxygen sensitivity and lack of spore formation, it seems that these taxa rely mostly on  
610 vertical transmission at birth, after which they persist indefinitely (152). Post birth, a  
611 significant fraction of the infant gut microbiota is derived from breast milk (first transport  
612 route of microorganisms by "food") during the first year of life. Breast milk may provide over  
613 800,000 bacterial cells per day, serving as pioneer colonizers of the infant's gut (155).  
614 Microbial signatures shared between breast milk and infant stools were 88% one week after  
615 birth, declining to 70% at week 12 (154). The percentage microbiome shared between mother  
616 and infant increased with frequency of breast milk consumption (157). Key shared  
617 microorganisms include *Escherichia/Shigella*, *Bifidobacterium longum*, *Bacteroides fragilis*,  
618 *Bacteroides thetaiotaomicron*, *Bilophila wadsworthia* and *Enterococcus faecalis* (158).

619 Many other animals exchange microorganisms in a similar way: for example, some of  
620 the calf fecal microbiota seem to derive from inoculation from the birth canal of the dam  
621 (159). Other routes of transmission can include the calf licking the dam, from the environment  
622 during and immediately after birth, and from the dam licking the calf clean immediately post  
623 birth. Taxa which showed the highest abundance in calf mouth samples taken within first 30  
624 minutes of life included *Acinetobacter* spp. and *Solibacillus* spp., also detected in fecal calf  
625 and cow samples. However, their abundance in fecal samples decreased with time (159).

626 Post-birth vertical transmission routes provide the first exposure of newborns to rich and  
627 diverse microbiomes and thereby provide the initial inoculum for the development of their  
628 own gut microbiome. Due the overall importance of a healthy gut microbiome for  
629 human/animal health and well-being, breast-feeding and similar exchanges represent highly  
630 important transmission routes of microbiomes.

631

632 **OTHER LIFESTYLE FACTORS WHICH INFLUENCE THE HUMAN**  
633 **MICROBIOME**

634 **The relevance of the environment and social interactions for microorganism transfer**

635 Environmental microorganisms are thought to play an important role in triggering the  
636 immune system at early stages of life, making the human immune system more resilient  
637 towards challenges as adults (160). Children growing up on farms, for example, are exposed  
638 to a high microbiome diversity from the environment, and subsequently develop a more  
639 diverse gut and body microbiome. Evidence suggests that such children are less prone to  
640 allergy development in later life than children from urban areas (161). The exposure of  
641 children to diverse food and environmental microbiomes is thus important (162), and is the  
642 basis of the ‘hygiene theory’ (163), i.e., an intimate connection between microbial diversity in  
643 the environment, microbial community structure and function at barrier organs of the human  
644 body and subsequent health and wellbeing, potentially via the interaction of microorganisms  
645 and the immune system (160).

646 Social interactions represent a route for microorganism exchange between individuals  
647 with systems-level implications. Studies in humans have shown that proximity and frequent  
648 social physical contact result in microorganism exchange. Individuals living together showed  
649 increased gut microbial diversity and abundance of potentially beneficial microorganisms  
650 (164, 165). Dill-McFarland et al. (164) reported that the salivary microbiome influences the  
651 gut microbiome, and that the salivary microbiome may be influenced by kissing. Also, there is  
652 evidence that oral and gut microbiota are shared in close social networks (mothers and infants  
653 and marital partners), as well between females but less between males (165). When  
654 comparing the gut microbiomes of spouses to those of sibling pairs, spouses had more  
655 microbial species in common than siblings, even after accounting for dietary factors (164).  
656 Humans sharing the same household, including unrelated individuals, harbored more similar  
657 gut microbiota than individuals living in different houses (166). A recent study by Valles-  
658 Colomer et al. (167) analyzed more than 9,700 human metagenomes and computational  
659 strain-level profiling revealed extensive bacterial strain sharing across individuals. Different  
660 transmission patterns were identified for mother-to-infant, intra-household, and intra-  
661 population transmission patterns. Overall, these findings indicate that social interactions are  
662 important in shaping the human microbiome, and that this factor may exert an even stronger  
663 influence than shared genetic factors and early life environments supporting previous findings

664 (164). The patterns observed within households extends to other socially shared spaces such  
665 as schools, workplaces, and public transportation (168).

666 From the current evidence for microbial interconnections between hosts and  
667 ecosystems, the concept of the social microbiome (collective metacommunity) has emerged. It  
668 is defined as the microbiome of a given group that can be transmitted horizontally across  
669 members of a group or acquired from the environment where it socializes (165).

670 Poor social integration relates to an increased risk of developing diseases, ranging from  
671 metabolic disorders to mental conditions. The links between alterations in the human  
672 microbiome and mental health (the gut-brain-axis) are well described (169). On this basis, it  
673 has been hypothesized that social life may bring health benefits (and sometimes disbenefits;  
674 SARS-CoV-2, for example) through microorganism transmission amongst members of a  
675 social group. Furthermore, microbiomes may influence the ability of their hosts to cooperate  
676 and interact, for example in displaying paternal care behavior (170). The connection between  
677 the gut and brain means that microbiomes can influence social behavior and decision-making  
678 through emotions and cognitive processes (171).

679 Theories about the implications of socialization in microbial transmission are still  
680 grounded on preliminary evidence. To date, only a few studies have controlled for relevant  
681 variables (dietary, environmental, and genetic), and even fewer have investigated microbial  
682 transmission via strain tracking and linked transmission with health outcomes. Yet emerging  
683 work on primate populations highlights the intimate connection between microbiota  
684 composition, functional links to immune status (e.g., anti-inflammatory taxa), and social  
685 behavior (172). Inevitably, some key research questions have emerged from animal and  
686 human studies: how social-microbial communities of (mammal) hosts participate in their  
687 selection by modifying the host's or the group's behavior, does this phenomenon transcend  
688 individual and closely living groups, and is there a role of co-evolution of humans and  
689 microbiomes of social behavior, demographic changes and global health?

690

### 691 **Exchange of microbiota between pets and humans**

692 Humans have been sharing living spaces and food resources with companion animals  
693 for millennia. Dogs were domesticated thirty thousand and cats ten thousand years ago.  
694 Humans and horses have been in close proximity for over six thousand years. Such long  
695 periods of mutual exposure have most likely enabled co-evolution of the microbiomes of both  
696 humans and animals: it is not just the pets that were domesticated, but their microbiomes, too.



697 Short-term studies have shown that co-habitation with pets results in an alteration of gut  
698 microbiota diversity and composition in both humans and animals (173). These alterations  
699 have functional implications. For instance, Du et al. (173) showed that cat ownership was  
700 associated significantly changed metabolic pathways, e.g., increased metabolism of amino  
701 acids, nucleotides, biological oxidation carbohydrates, vitamins and lipids. Also, intriguing  
702 interactions were observed for microbiome exchange between cats and their owners with  
703 respect to the gender and physiology of owners. To this end, differences in the exchange of  
704 different bacterial families from cats to human females and males have been observed, and  
705 between feline pets as well as between healthy and overweight owners (173).

706 Wetzels et al. (174) analyzed skin bacterial communities of wolves and dogs living in  
707 outdoor packs and compared these with human care-takers and their pet dogs. Even though  
708 humans had more distinct and less diverse bacterial communities than other studied groups,  
709 bacterial communities of individuals in close contact with outdoor pack animals showed more  
710 similarities to the bacterial communities of these animals. In particular, both the ratio of  
711 Gram-negative to Gram-positive microorganisms on the skin and the phylum level diversity  
712 were increased.

713 The intimate relationship between pets and owners potentially represents a public health  
714 concern in terms of AMR genes development and transmission (173). Indicative evidence has  
715 been provided in several studies where AMR genes present in fecal samples of humans and  
716 their companion animals were characterized (176-178). In a more comprehensive  
717 metagenomic study, Zhao et al. (179) compared the gut AMR genes, the MGEs and the  
718 microbiota among dogs and their owners as well as kennel dogs. Owned dogs shared 70% of  
719 AMR genes with their owners, whereas only 52% of observed AMR genes were shared  
720 between kennel dogs and owners. More detailed analysis focusing on dog-owner pairs has  
721 indicated that AMR genes, MGEs and microbiota composition correlated significantly with  
722 each other. The shared microbiome (*sensu* bacterial community) between the owner and pet  
723 was considered to be the main basis of the co-occurrence in AMR genes. Despite the  
724 increasing knowledge of the microbiome exchange between pets and their owners involving  
725 also the exchange of AMR genes, little understanding exists on the functional consequences  
726 of these transfer events.

727

728 **Microorganism transfer in the built environment**

729 Buildings are typically complex ecosystems that not only provide shelter for their  
730 inhabitants, but also harbor trillions of microorganisms that can interact with each other (180).  
731 The two primary mechanisms of microbiome transfer in the built environment are (1)  
732 bioaerosols, and (2) via physical contact/exchange from surfaces.

733 As outlined earlier in this review, bioaerosols are airborne particles of biological origin.  
734 They can include bacteria, fungi, archaea, viruses, pollen, and their cell wall components  
735 and/or metabolic products. Overall, bioaerosols can be considered as an imprint of the  
736 environment (51) where they derive from. They are important in the transmission of  
737 pathogenic organisms to plants, animals, and humans, resulting in the spread of diseases  
738 within populations (182).

739 In built environments, the quantity of air circulation and the type of environment will  
740 affect the mechanism and magnitude of the transfer of microorganisms via bioaerosols (182).  
741 For instance, Triadó-Margarit et al. (183) showed that 22% overlap of bacterial taxa in  
742 microbiomes found in different locations of the Barcelona subway, such as inside trains, the  
743 platform, or the lobby. This is indicative of the flow of microorganisms between different  
744 locations.

745 Fungal spores are efficiently spread in many environments. While airborne spores of  
746 pathogens such as *Aspergillus fumigatus* are typically inhaled without harmful consequences,  
747 for immunocompromised people, airborne fungal spores may result in invasive aspergillosis  
748 or skin infections (184). Similarly, immunocompromised patients can more readily acquire  
749 fungal skin infections caused by dermatophytic fungi. Dermatophytic fungi were shown to  
750 have a set of keratin-degrading enzymes, enabling them to invade through the skin of humans  
751 or animals (185). In contrast, healthy skin microbiota (particularly bacteria and yeasts) do not  
752 have such set of keratin-degrading proteases (185).

753 Residents leave their microbial fingerprint mainly from their skin (186), but less is  
754 known about the transfer of microbiota plants to the built environment. First indications that  
755 plants substantially contribute to the microbial abundance and diversity in the built  
756 environment were found in a study on the surface microbiome of intensive care units of a  
757 university hospital (187). Transfer of microorganisms from plants to surfaces in a building  
758 may be mediated by window ventilation. Kembel et al. (180) showed that the phylogenetic  
759 diversity of airborne bacterial communities was lower indoors than outdoors, and  
760 mechanically ventilated rooms contained less diverse microbial communities than window-  
761 ventilated rooms (180). The initial observations were later experimentally confirmed by

762 analyzing the microbiome of the spider plant *Chlorophytum comosum* and its surrounding  
763 environment (188). The abundance of archaea, bacteria, and fungi increased on the floor and  
764 wall surfaces near the plant within six months, whereas the microbial abundance on plant  
765 leaves and in the indoor air remained stable. Moreover, a clear shift in the composition of the  
766 microbiota was observed; bacterial diversity on surfaces increased significantly while fungal  
767 diversity decreased. This study demonstrated for the first time that indoor plants can alter the  
768 microbiome of a built environment, which supports the significance of plants and provides  
769 insights into the complex interplay of plants, microbiomes, and human beings (188).

770 Kozdrój et al. (182) evaluated the exposure of visitors and workers to airborne bacteria  
771 and fungi at different botanical garden sites, including within the garden glasshouses. Not  
772 surprisingly, the concentrations of bioaerosol microbiota and their diversity were higher in the  
773 glasshouses compared to those found in the outdoor air of the garden area. The bacterial taxa  
774 present in adjacent streets were also found in the glasshouse and garden, suggesting  
775 substantial microorganism exchange.

776 Exposure to diverse environmental microbiota has been suggested to confer protection  
777 against immune-mediated disorders (189). For example, vegetation around homes was shown  
778 to be associated with health-related changes in gut microbiota composition suggesting a  
779 transmission route via built environments (190). However, additional studies will be required  
780 to understand how to specifically utilize indoor plants to modulate the indoor microbiota for  
781 health benefits. Interestingly, such potential links equally inspire scientists and artists, in the  
782 attempt to define human identity in the broader perspective of the surrounding environment  
783 and biosphere (191).

784 Transfer of microorganisms from the built environment to humans is particularly  
785 impactful in the hospital environment. According to the World Health Organization, 7 – 15%  
786 of patients in acute-care hospitals acquire at least one healthcare-associated infection during  
787 their hospital stay, often with severe or fatal outcomes that are augmented when resistant  
788 microorganisms are involved (192). Recently, the persistence of pathogens on inanimate  
789 surfaces was reviewed (193) and direct transfer to patients was demonstrated in several  
790 studies. Cason et al. (194) used whole genome sequencing-based typing of vancomycin-  
791 resistant enterococci to analyze the genetic relationships between bacterial isolates originating  
792 from patients and the hospital environment. Five out of eight identified clusters of closely  
793 related strains ( $\leq 3$  alleles differing between the genotypes) contained both environmental and

794 patient isolates, providing strong evidence of the exchange of microorganisms between  
795 hospital environments and humans.

796 Microbiomes in the built environment and their dispersal in bioaerosols have only been  
797 recently recognized as an important issue for human health. Apart from the transmission of  
798 pathogens or allergenic molds, air-borne microorganisms are also likely to beneficially  
799 influence human health and well-being, e.g., by out-competition or antagonism of pathogens.  
800 Microbiome dynamics in the built environment and its impact on air quality requires further  
801 understanding, and bioaerosol microbiomes may be subject of new approaches to improve the  
802 health and well-being of humans in their home and working environments.

803

#### 804 **Microbial transmission from humans to the environment**

805 Vast numbers of microorganisms (primarily prokaryotes) are discharged from humans  
806 to wastewater treatment plants. Typically, 0.5 kg feces are discharged per person per day,  
807 with each gram containing  $10^9$  bacterial cells: i.e.,  $\sim 5 \times 10^{11}$  bacterial cells per person per day.  
808 With a world population of 7.8 billion people,  $3.9 \times 10^{24}$  bacterial cells are released from  
809 humans into the environment daily, from fecal waste alone.

810 Given the sheer numbers of bacteria discharge by humans, perhaps it is no surprise  
811 there are overlaps between the microbiomes of the human gastrointestinal tract, municipal  
812 sewer systems (195) and municipal wastewater treatment plants (196). For example,  
813 phylogenetically related members of the family *Lachnospiraceae*, which currently comprises  
814 80 genera and 176 species (<https://lpsn.dsmz.de/family/lachnospiraceae>), have been recovered  
815 from both human feces and environmental samples (197).

816 A unique example of horizontal inter-kingdom transfer of a human opportunistic  
817 pathogen (*Propionibacterium acnes*) to the domesticated grapevine (*Vitis vinifera* L.) was  
818 shown by Campisano et al. (198). The authors showed that this bacterium colonizes different  
819 plant tissues, such as bark and inside pith tissues, both inter- and intra-cellularly. Phylogenetic  
820 and comparative genomics analyses indicated that the establishment of the grapevine-  
821 associated *P. acnes* as an obligate endophyte was due to a recent transfer event, likely during  
822 the Neolithic period when the grapevine was domesticated.

823

#### 824 **THE EXCHANGE OF VIROMES BETWEEN ENVIRONMENTS**

825           The COVID-19 pandemic has focused attention on the role and impact of the  
826 environmental virome on human health, socio-political and economic systems and on  
827 planetary health. During the COVID-19 pandemic, the testing of municipal wastewater by  
828 qPCR and genome sequencing were invaluable in the surveillance and informed responses to  
829 the disease. These tools allowed science to inform decision-making which directly impacted  
830 human health and wellbeing, while seeking to maintain essential services and business where  
831 possible. The application of these tools enabled estimating the extent of SARS-CoV-2  
832 infection within populations, and determining the relative abundance of genetic variants that  
833 arose over time (e.g., 199).

834           To better understand viral transfer processes, virome surveillance can potentially be  
835 applied in more generalized manner, for example to educational institutions, long-term care  
836 facilities and hospitals, cruise ships, farms, airports and aircraft (200). The technology and  
837 approaches are widely applicable to human and animal viruses, whether they be RNA viruses,  
838 such as SARS-CoV-2, or DNA viruses, such as monkey pox (201).

839           Viruses that impact human health directly are of high priority. However, human health  
840 is dependent on a safe and abundant food supply. As such, environmental virome surveillance  
841 is an emerging tool for detection of virus outbreaks more broadly. Shotgun metagenomics  
842 analysis has revealed that the most abundant RNA viruses in municipal wastewater, by far,  
843 are plant viruses such as the widespread tobamoviruses (202). These infect a wide range of  
844 common crop plants, and new variants commonly arise (e.g. the Tomato Brown Rugose Fruit  
845 Virus; 203). The presence of these plant viruses is almost certainly of dietary origin, rather  
846 than agricultural sources such as runoff from vegetable greenhouse operations. This suggests  
847 that the incidence and distribution of viruses infecting crop plants is far greater than  
848 previously thought. Routine surveillance through testing of plant tissue samples would be  
849 laborious and would suffer from inadequate coverage. Alternatively, sampling of the  
850 proximate environment such as irrigation runoff has the potential to detect viruses and other  
851 pathogens far more effectively.

852           Viromes in the environment are still poorly understood, however, the COVID-19  
853 pandemic and other viral diseases have increased the awareness of their importance. Virome  
854 transfer may not only indicate the presence of a disease but may also induce microbiome  
855 changes in the receiving environment with yet unknown effects on ecosystem functioning.

856

857 **MICROBIOME ESTABLISHMENT AND ADAPTATION IN NEW**  
858 **ENVIRONMENTS**

859 Establishment of microorganisms in new ecosystems occurs via a phased process (204):  
860 first, microorganisms have to be transferred to a new habitat via microbial dispersal (i.e., by  
861 horizontal or vertical transmission). Then, the introduced microorganisms need to establish  
862 and adapt to their new environments which may, or may not, lead to a viable and self-  
863 sustaining population. As the system stabilises and processes such as initial environmental  
864 filtering have been completed, the importance of longer-term environmental selection and  
865 species competition become stronger (205).

866 Establishment of new microorganisms and re-assembly of microbiomes in a new  
867 ecosystem mainly depend on the selectivity of the environmental conditions, the original  
868 structure of the microbiome, the dilution rate upon transfer, the availability of free ecological  
869 niches in the place of transfer, and the evolutionary capacity and fitness of the transferred  
870 strains. Selectivity of the new environmental conditions spans a continuum of neutral to  
871 highly selective; these have differing impacts depending on microbial diversity (205). For  
872 example, in the case of the soil microbiome, it has been shown that soil pH is a key predictor  
873 of microbial community structure before or after transfer (7). In human milk, oligosaccharides  
874 may act as a selective factor for the outgrowth of *Bacteroides* spp. and *Bifidobacterium* spp.  
875 upon maternal fecal microbiota transplantation to Caesarean-born infants (206). Most  
876 fermented foods go through ecological succession with early growth of prevailing  
877 autochthonous bacteria. As the pH of the food decreases, overgrowth of LAB occurs (207).  
878 Refeeding of sourdough (back-slopping propagation) shapes the microbiome and selects  
879 specific LAB species depending on the age and other parameters of the starter and receiving  
880 materials. For example, *Fructilactobacillus sanfranciscensis* is a dominant species in mature  
881 wheat and rye sourdoughs with short fermentation times, whereas more acid-tolerant  
882 *Limosilactobacillus reuteri* is found in sourdough with long fermentation cycles at higher  
883 temperatures (208).

884 The resident microbiome may prevent the colonization of newcomers in the ecosystem  
885 by providing resistance and competition against the intruders, which is well known for the  
886 establishment of pathogens. For example, pathogens do not readily establish in soils due to  
887 soil suppression (209). Likewise, in the human gut, the microbiome prevents the  
888 establishment of pathogens via colonization resistance (210). Both processes are mediated by  
889 the resident microbiome.

890 The availability of unoccupied niches in the place of transfer may increase the  
891 likelihood of invasion by transferable microorganisms. Availability of niches to occupy can  
892 enable direct colonization or adaptive radiation processes. This is observed in the efficacy of  
893 fecal transplantation treatments for patients suffering from recurrent infection with  
894 *Clostridioides difficile*. In these patients, the very low diversity of colonic microbiota with  
895 limited microbial interaction networks enables higher transplantation success – and better  
896 health outcomes – than for patients non-intestinal infectious diseases (211). Success of the  
897 transplantation also depends on the characteristics of the donor’s microbiota when comparing  
898 subjects with the same condition (212). The outcome of microbiome transfer also depends on  
899 the size of the transferable aliquot. A dilution effect could significantly reduce the taxonomic  
900 and functional diversity of re-assembled bacterial communities (213).

901 Upon transfer to the new environment individual microbiome members can become  
902 maladapted. At the strain level, adaptation to new conditions could include alteration of the  
903 physiological state, HGT, or the selection of new mutations. The process of strain adaptation  
904 to the new environment depends not only on intrinsic abilities of the strain (e.g., genome size  
905 and encoded life strategies), but also on the members of the surrounding community. It has  
906 been shown that there is stronger evolutionary response in low-diversity communities (214).

907 Microbiome establishment is key to a long-lasting microbiome transfer. It is therefore  
908 not only important to understand how individual strains can establish but also how a complex  
909 microbiome can establish and how this is influenced by microbial interactions or  
910 environmental effects.

911

## 912 **CONCLUDING REMARKS**

913 The ecology and functioning of microbial communities are typically studied in one  
914 specific environment at a time, and microbiome transmission between different environments  
915 has been generally overlooked. Most studies on microbiome transmission have addressed  
916 horizontal or vertical transmission routes of microbiomes associated with higher organisms  
917 such as humans (166, 167), plants (19, 27) or insects (68, 76). Also, transmission routes of  
918 pathogens and of AMR genes have been investigated in some detail, particularly the transfer  
919 from primary habitats to those affecting human health. However, microbiome connectivity  
920 between different environments is vast (Figure 1) and has a magnitude that has been little  
921 considered or understood.

922 Some transmission events have detrimental effects such as the transmission of  
923 pathogens, whereas many microbiome connections have positive effects on ecosystem  
924 functioning or human health (Figure 2). Examples of the positive effects of microbiome  
925 transfer include the methods used to establish diverse and healthy human gut microbiomes  
926 (probiotic treatments, fecal transplants (211, 214).

927 It is evident that microbiome transmission between environments occurs continuously  
928 and between most environments on Earth (Figure 1). Considering the ubiquitous nature of  
929 microbiome transfer, we can reasonably assume that the consequences of microbiome transfer  
930 on global ecosystem functioning and the health of our planet are very large, even if we do not  
931 yet fully understand the magnitude of the process.

932 As microbiomes play key roles in most if not all global environments, the fluidity of  
933 microbiome diversity and composition may be associated with a gain or loss of functions,  
934 with potentially positive or negative consequences for the environment. Transmission of  
935 microbiomes can provide a mechanism for ecosystem or holobiont adaptation. For instance,  
936 plants receiving new microbiome members from other plants, soils, insects or bioaerosols  
937 may acquire positive attributes such as increased pathogen or stress resistance. Similarly, the  
938 human acquisition of microorganisms from other humans, animals or pets, plant-derived food  
939 or even bioaerosols may affect their immune status or even social behavior.

940 The development of high-throughput nucleic acid sequencing technologies has  
941 facilitated the rapid analysis of complex microbiomes and their transfer between  
942 environments. While the majority of such studies are based on amplicon sequencing of  
943 phylogenetic markers, there is an increasing trend of whole metagenome analysis (e.g., 168).  
944 Metagenome-based studies make it possible to investigate the functional potential of  
945 microbiomes, but also facilitate strain-level profiling of microbiomes. The latter is important  
946 for investigations of the transmission of individual strains; e.g., either pathogens (such as  
947 specific outbreak strains) or beneficial microbiota. Metagenome information may be also used  
948 to study the effect of MGEs on the transmission of particular traits; e.g., those enhancing  
949 ecological competence in the new environment.

950 There is a critical need to link microbiome and metagenome information with  
951 phenotypic or functional data to better understand the functional consequences of microbiome  
952 transmission events for the microbial community as well as the ecosystem/host.  
953 Metatranscriptomics of source and sink communities can address the issues of gain or loss of  
954 functionality during or after transfer events. Other ‘omics’ approaches, including



955 metaproteomics, metabolomics and high throughput cultivation, can all generate critical  
956 information on microbiome functionality.

957 It is widely accepted that a more holistic approach understanding microbiome  
958 transmission processes would be advantageous, even if technically demanding. Given that  
959 most microbiomes contain taxa from all three kingdoms; e.g., bacteria, fungi, protozoa,  
960 archaea and viruses, in addition to MGEs, and given that many of these may interact in  
961 multiple, complex and poorly understood ways, a multi-taxon approach to studying  
962 microbiome transfer processes is likely to reveal novel and potentially exciting results. There  
963 is also yet limited knowledge of the adaptation processes of individual microbiome members  
964 upon transfer to a new and different environment.

965 The fact that microbiomes of different environments are connected and exchanged  
966 needs to be considered in global practices such as agricultural management. Microbiome  
967 interconnectedness also has potential to be used as an approach to modulate microbiomes in  
968 the selection or provision of desirable traits. For instance, the human gut microbiome could be  
969 modulated by “designing” plant microbiota of plant-derived food (e.g., fermented food or  
970 salads). Similarly, plants enriched in probiotic strains could help to enrich bioaerosols to  
971 support the human immune system, supporting the respiratory system or skin functions. Such  
972 microbiota-enriched plants could potentially be used in the built environment; on green walls  
973 or other type of plant ‘installations’. As there is a connection between microbiomes,  
974 atmosphere and dispersal, local weather, and global climate, it is important to increase our  
975 understanding of the role microorganisms have in hydrological cycles, and how phyllosphere  
976 microorganisms impact and are impacted by weather. Such advanced understanding will not  
977 only help to quantitate the role of microorganisms in the global climate but may assist in the  
978 design of novel strategies employing transferrable microbiomes to define new solutions for  
979 improving the human health and the health of our planet.

980

## 981 **ABBREVIATIONS**

982 AMR - antimicrobial/antibiotic resistance; HGT - horizontal gene transfer; LAB - lactic acid  
983 bacteria; MGE - mobile genetic element

984

985

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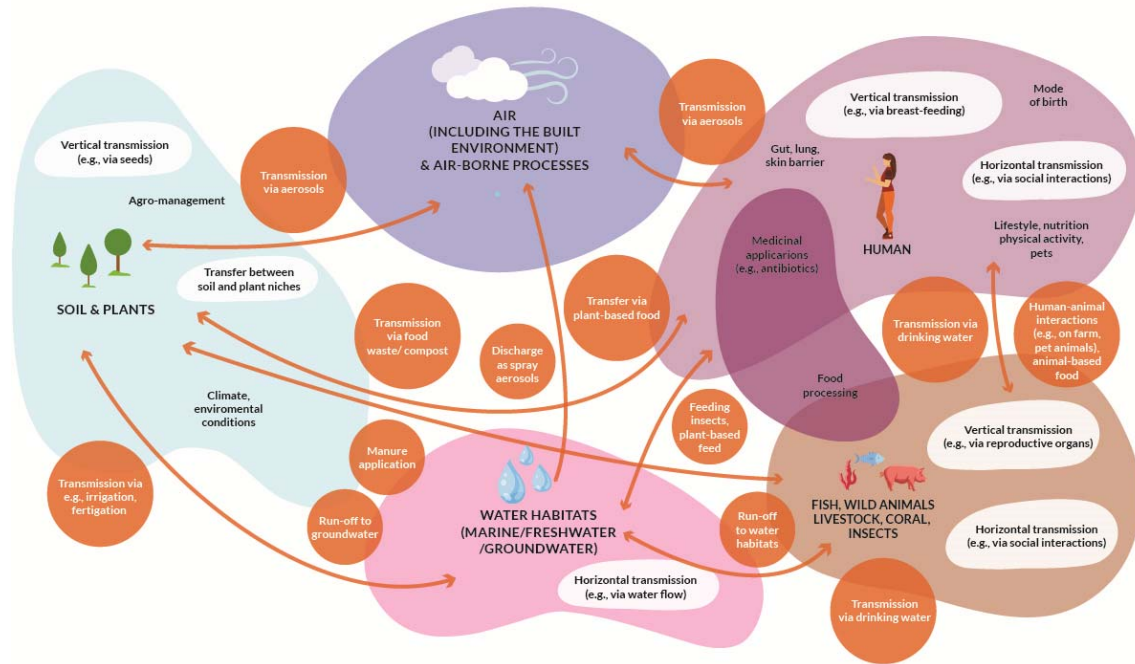
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995 FIGURES

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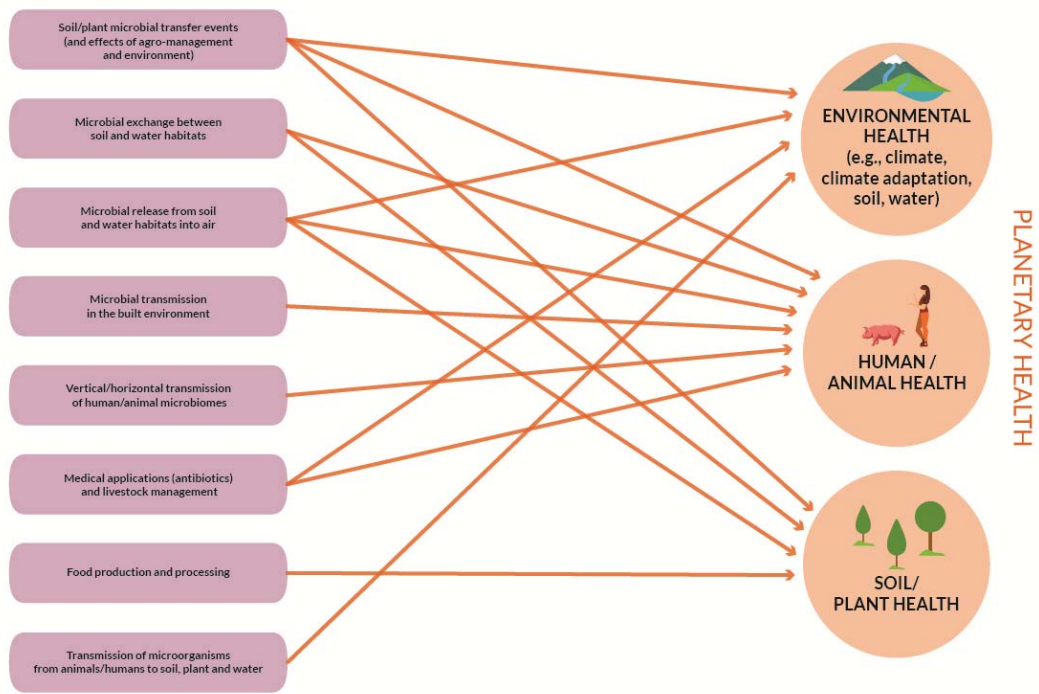


998

999 **Figure 1.** Microbiome transfer between environments and modes of transfer

1000

1001



1002

1003 **Figure 2.** Microbiome connectivity between environments and impact on environmental  
 1004 health, human/animal health and plant health

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