

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

3
4 Angela Sessitsch^{1*}, Steve Wakelin², Michael Schloter³, Emmanuelle Maguin⁴, Tomislav
5 Cernava⁵, Marie-Christine Champomier-Verges⁴, Trevor C. Charles⁶, Paul D. Cotter⁷, Ilario
6 Ferrocino⁸, Aicha Kriaa⁴, Pedro Lebre⁹, Don Cowan⁹, Lene Lange¹⁰, Seghal Kiran¹¹, Lidia
7 Markiewicz¹², Annelein Meisner¹³, Marta Olivares¹⁴, Inga Sarand¹⁵, Bettina Schelkle¹⁶,
8 Joseph Selvin¹¹, Hauke Smidt¹⁷, Leo van Overbeek¹³, Gabriele Berg¹⁸, Luca Cocolin⁸,
9 Yolanda Sanz¹⁴, Wilson Lemos Fernandes Jr¹, SJ Liu¹⁹, Matthew Ryan²⁰, Brajesh Singh²¹,
10 Tanja Kostic¹

11
12
13 ¹AIT Austrian Institute of Technology GmbH, Tulln, Austria (angela.sessitsch@ait.ac.at,
14 wilson.fernandes-lemos@ait.ac.at; anja.kostic@ait.ac.at)

15 ²Scion, Christchurch, New Zealand (steve.a.wakelin@scionresearch.com)

16 ³Helmholtz Zentrum München, Oberschleissheim, Germany (schloter@helmholtz-
17 muenchen.de)

18 ⁴Université Paris-Saclay, INRAE, AgroParisTech, Micalis Institute, Jouy-en-Josas, France
19 (emmanuelle.maguin@inrae.fr, marie-christine.champomier-verges@inrae.fr,
20 aicha.kriaa@inrae.fr)

21 ⁵University of Southampton, Faculty of Environmental and Life Sciences, Southampton, UK
22 (t.cernava@soton.ac.uk)

23 ⁶University of Waterloo, Waterloo, Canada (tcharles@uwaterloo.ca)

24 ⁷Teagasc Food Research Centre, Moorepark, APC Microbiome Ireland and VistaMilk, Cork,
25 Ireland (paul.cotter@teagasc.ie)

26 ⁸University of Turin, Grugliasco, Italy (ilario.ferrocino@unito.it;
27 lucasimone.cocolin@unito.it)

28 ⁹University of Pretoria, Pretoria, South Africa (pedro.bixiraonetomarinholebre@up.ac.za;
29 don.cowan@up.ac.za)
30 ¹⁰LL-BioEconomy, Valby, Copenhagen, Denmark (lene.lange2@gmail.com)
31 ¹¹Pondicherry University, Puducherry, India (seghalkiran@gmail.com;
32 josephselvinss@gmail.com)
33 ¹²Institute of Animal Reproduction and Food Research of the Polish Academy of Sciences,
34 Department of Immunology and Food Microbiology, Olsztyn, Poland
35 (l.markiewicz@pan.olsztyn.pl)
36 ¹³Wageningen University & Research, Wageningen Research, Wageningen, The Netherlands
37 (annelein.meisner@wur.nl; leovanoverbeek@wur.nl)
38 ¹⁴Institute of Agrochemistry and Food Technology, Excellence Center Severo Ochoa -
39 Spanish National Research Council (IATA-CSIC), Valencia, Spain (m.olivares@iata.csic.es;
40 yolsanz@iata.csic.es)
41 ¹⁵Tallinn University of Technology, Department of Chemistry and Biotechnology, Tallinn,
42 Estonia (inga.sarand@taltech.ee)
43 ¹⁶European Food Information Council, Brussels, Belgium (bettina_schelke@hotmail.com)
44 ¹⁷Wageningen University & Research, Laboratory of Microbiology, Wageningen, The
45 Netherlands (hauke.smidt@wur.nl)
46 ¹⁸Graz University of Technology, Graz, Austria, (gabriele.berg@tugraz.at)
47 ¹⁹Chinese Academy of Sciences, Institute of Microbiology, Beijing, China (liusj@im.ac.cn)
48 ²⁰Genetic Resources Collection, CABI, Egham, UK (m.ryan@cabi.org)
49 ²¹Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South
50 Wales 2751, Australia (B.Singh@westernsydney.edu.au)

51

52 *corresponding author

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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 2×10^8 and 1×10^9 km² (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 (≤ 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, 3.9×10^{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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992

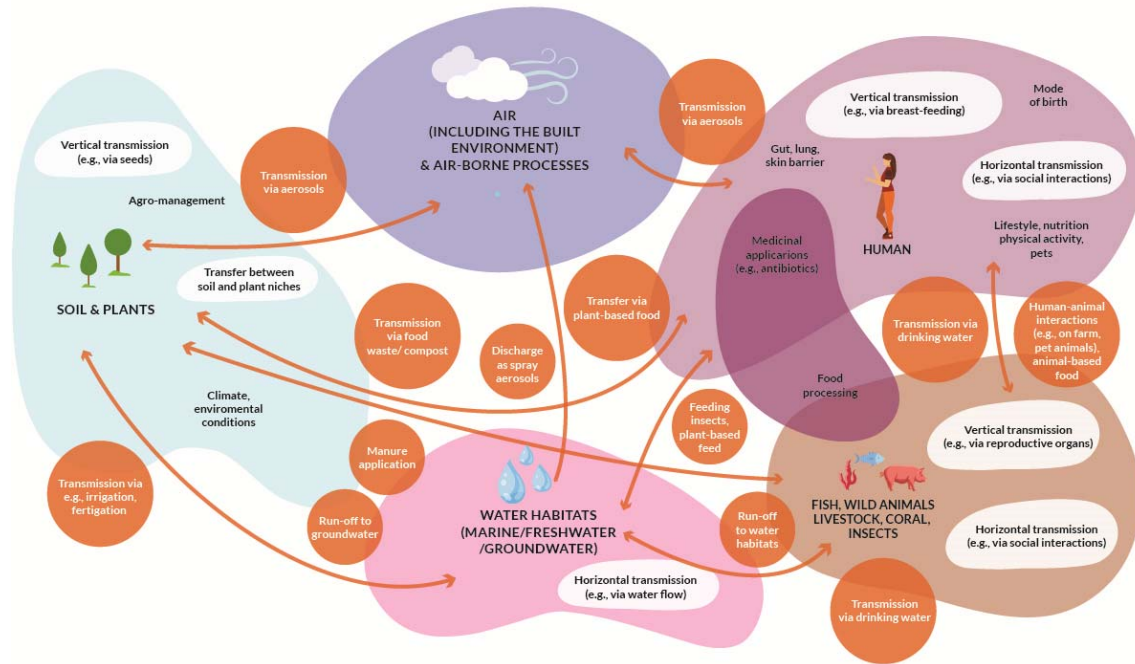
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995 FIGURES

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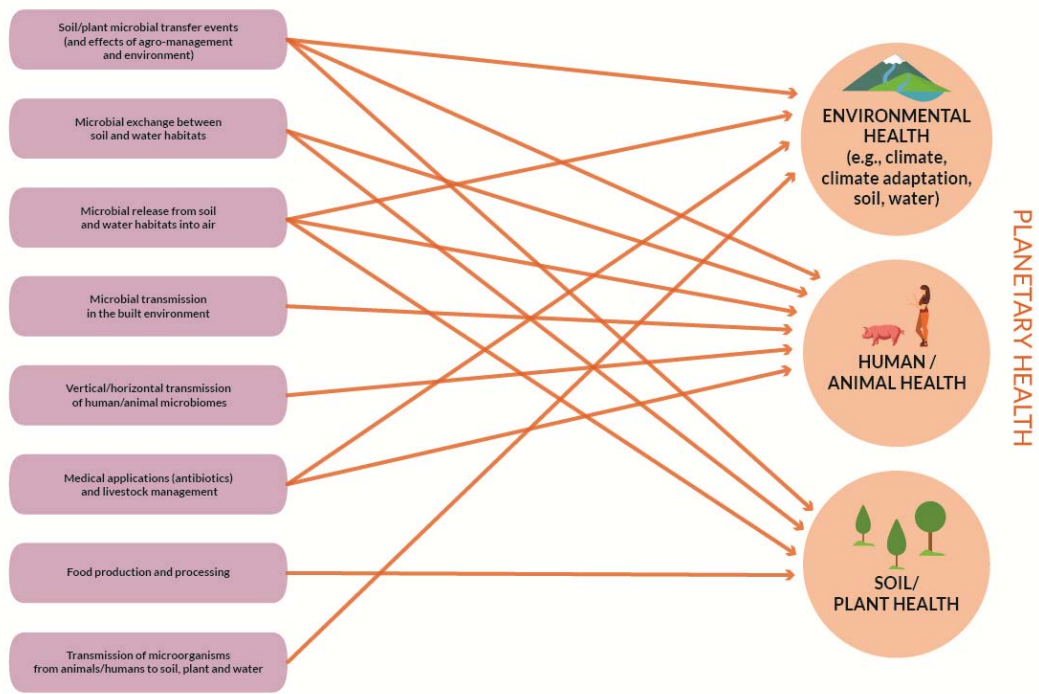


998

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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