Microbiotic particles in water and soil, water-soil microbiota coalescences, and antimicrobial resistance

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Abstract

Bacterial organisms like surfaces. Water and soil contain a multiplicity of particulated material where bacterial populations and communities might attach. Microbiotic particles refers to any type of small particles (less than 2 mm) where bacteria (and other microbes) might attach, resulting in medium- long-term colonization. In this work, the interactions of bacterial organisms with microbiotic particles of the soil and water are reviewed. These particles include bacteria-bacteria aggregates, and aggregates with particles of fungi (particularly in the rhizosphere), protozoa, phytoplankton, zooplankton, biodetritus resulting from animal and vegetal decomposition, humus, mineral particles (clay, carbonates, silicates), and anthropogenic particles (including wastewater particles or microplastics). At they turn, these particles might interact and coalesce (as in the marine snow). Natural phenomena (from river flows to tides, tsunamis, currents, or heavy winds) and anthropogenic activity (such as agriculture, waste-water management, mining, soil-mass movement) favors interaction and merging between all these soil and water particles, and consequently coalescence of their bacterial-associated populations and communities, resulting in an enhancement of mixed-recombinant communities capable of genetic exchange, including antimicrobial resistance genes, particularly in antimicrobial-polluted environments. Particles also favor compartmentalization of bacterial populations favoring diversification and acquisition of mutational resistance by random drift. In general, microbial evolution is accelerated by the aggregation of microbiotic particles. We propose that the world spread of antimicrobial resistance might relate with the environmental dynamics of microbiotic particles, and discuss possible methods to reduce this problem influencing One Health and Planetary Health.

Key-Words: Microbiotic particles, Antimicrobial resistance, Water particles, Soil particles, particles coalescence

Introduction

Bacteria like surfaces. Surfaces create compartments, where organic molecules, microorganisms, and pollutants can concentrate, fragmenting the apparent homogeneity of water bodies, and making it difficult or impossible to accurately prediction of environmental health risks (Burkart, 2000). On the other hand, these concentrating patches are a prerequisite for the formation of chemical gradients in the homogeneous (non-compartmentalized) space, which to a certain extent (until the limit of diffusion) are converted into their satellite “domains”. Compartmentalization contributes to the subdivision of bacterial populations that can colonize various patches (metapopulations), and (depending on the time of occupancy and the local selection) give rise to phenotypical or genotypical differentiation. The random bacterial occupation of micro-compartments might on the other hand favor drift evolution, providing opportunities to minorities that could have low possibilities of fixation in fully homogeneous environments.

Bacterial genetic diversification is believed to result from spontaneous tendency for differentiation (and therefore populational complexification) arising from the sequential accumulation of random events over time. This theory is postulated by the “zero-force evolutionary law” stating that in any evolutionary system in which there is variation and heredity there is, in the absence of constraints, a random tendency for diversity and complexity to increase (McShea and Brandon, 2010). In fact, this tendency is a consequence of the second law of thermodynamics, in this case, increasing randomness in the molecular evolution of bacterial sequences over time (Wang et al., 2016).

As suggested previously, however, not only time, but space constitutes the framework for evolution. In fact, time is required to gain spaces, which are needed to gain time. The reasons for the biological “hunger for time” (reproduction, survival) are a not-irrelevant philosophical question (Arenhart 2019; Baquero, 2005). However, differentiated spaces, compartments, are as critical as time in evolutionary dynamics. Organisms expanding in these spaces foster their evolutionary capabilities. This review proposes that the world spread of antimicrobial resistance can relate with the environmental dynamics of microbiotic particles, forming compartmentalized spaces where bacterial cells of different origin, frequently of different species, co-aggregate and interact. Such coalescence spaces constitute a wealth of "evolutionary reactors" for the evolution of antimicrobial resistance (Baquero et al., 2008).

Surfaces, particles, and compartmentalized biospaces

In addition to liking to live on surfaces, all living organisms like surfaces and themselves provide surfaces. The extension of the external surface of an average bacterial cell is about 5-10 times the surface where the cell is deposited. In water systems, a wealth of particles providing attachment surfaces for microorganisms are available. These surfaces serve as condenser nodes for multiple bacterial species, thereby creating biospaces, Which are essentially a type of nest with an interwoven scaffolding structure determined by physico-chemical attractants fostering bacterial adhesion to surfaces. These attachment surfaces are of biotic and abiotic nature, and the result of attachment is the formation of a biotic particle. Adhesion surfaces for microorganisms in water and soil environments include surfaces of prokaryotic or eukaryotic organisms (Simon et al., 2002). Frequently, bacterial attachment to surfaces is followed by the construction of biofilms, which result from the release of extracellular polymers, such as polysaccharides. In this paper, we will essentially focus on microbiotic particles, ranging in average size from 5 µm to 5 mm in diameter and composed by, or carrying, bacterial organisms.

Bacteria-bacteria microbiotic particles

Bacterial surfaces promote inter-bacterial homogenic or heterogenic adhesion, involving the same or different species. Homogenic adhesion occurs within the same clonal population, forming spontaneous aggregates in the growing process. In Gram-positive organisms, many genera form spontaneous aggregates in liquid media (classical examples include *Staphylococcus*, *Streptococcus*, *Micrococcus*, *Enterococcus*, *Sarcina*, *Bacillus*, *Listeria*, *Corynebacterium*, *Mycobacterium,* and *Streptomyces*). Aggregates also occurs in Gram-negative bacteria, typically mediated by trimeric autotransporter adhesins in the outer membrane (Bassler et al., 2015; Adlakha et al., 2019). Mechanisms of auto-aggregation (same species) has been recently reviewed (Nwoko and Okeke, 2021). In water environments, bacterial “flocs” might be integrated by one or more species, have being designed “suspended bacterial aggregates” (Cai, 2020), and constitute an intermediary step in adhesion to other biotic or abiotic surfaces, forming colonies or biofilms (Vlamakis et al., 2013). Homogeneous biofilms also provide “surfaces” able to adhere new bacterial cells, giving rise to multi-microbial compartmentalized consortia: complex biofilms (Katharios-Lanwermeyer et al., 2014). Such bacterial complex coaggregates could evolve to become a “unit of selection” (Okasha, 2006; Baquero et al., 2021). that is, to a permanent assembly of organisms linked by cooperative or mutualistic interactions, leading to synergistic integrated functions in the ecosystems, as will be discussed later.

Microalgae-bacteria microbiotic particles

Microalgae eukaryotic cells, a main part of phytoplankton, are surrounded by a chemical “phycosphere” (Bell and Mitchell,1972), which can be colonized by microorganisms, ensuring a spatial long-term coexistence with bacterial groups, based on a complex interactive network of metabolites and signaling molecules(Seymour et al., 2017; Cirri and Pohnert, 2019) Most bacteria associated with microalgae, typically diatoms, are Proteobacteria and Bacteroidetes, which are also frequently linked to green algae. (Amin et al., 2012; Ramanan et al., 2016). During cyanobacterial blooms both Firmicutes and Proteobacteria increase in frequency (Zhang Weizhen et al., 2019).

Microfungi-bacteria microbiotic particles

It has classically been considered that fungi are infrequently found in water, although can be been detected in deep see sediments (Damare and Raghukumar, 2008). In most cases, these fungal species also occur in soil and freshwater environments, suggesting a terrestrial origin (Rédou et al., 2015). However, more recent studies indicate a high fungal biomass in the oceans, including the artics, approaching the bacterial biomass (Hassett et al., 2019).Many of these microfungi (such as Chytridiomycota) are also found in soil and freshwater. In fact, microscopic fungi are frequenty present in soil, particularly associated with the plant rhizosphere, where they closely and permanently interact with specific bacterial communities. Incidentally, these might play a role in triggering the germination of fungal spores (Scherlach et al., 2013). Such aggregates modulate the mycorrhizal symbiosis, a type of positive interaction reflected in the concept of ‘mycorrhiza helper bacteria” (Frey-Klett et al., 2007). Kin recognition and cooperation among bacteria occurs in spatially structured *Rhizobium* populations (Zee and Bever, 2014). During periodic or accidental merging of soil and water bodies, such functional fungal-bacterial particles can enter the water environment. Out of mycorrhizal space, fungal-bacteria interactions in the soil are frequently antagonistic (Bahram et al., 2018), probably preventing permanent particulated coaggregates. Macrofungi as Ascomycota and Basidiomycota, which seem to be important ecological players in all aquatic ecosystems (Grossart et al., 2019), contribute to the formation of bacterial-colonizable particles as those resulting from leaf litter decomposition (Zhao et al., 2021).

Protozoa-bacterial microbiotic particles

Amoeba are frequent protists in soil and water, usually grazing bacteria, but eventually preserving them, using a kind of “primitive agriculture” behavior (Brock et al., 2011). Social amoeba, such as *Dictyostelium discoideum* can form multicellular aggregates, and these particles incorporate living bacteria; in fact bacterial organisms can also kill and grow at the expenses of dead amoebas (Pukatzki et al., 2002; Bahram et al., 2018; Nguyen et al., 2020). Slime molds (myxomycetes) are composed of aggregates of amoebal organisms fused in a large cell (plasmodia) by the centripetal attraction of a signaling agent, acrasin. Many types of bacteria, mostly belonging to Proteobacteria, have been found to be associated with these plasmodia (Shu et al., 2018).

Zooplankton-bacterial microbiotic particles

Similarly, zooplankton constitute a large compartmentalized biospace harboring permanent bacterial communities; for example colonizing the exoskeleton and/ or gut of crustacean plankton (de Corte et al., 2018). The microbiota associated with *Daphnia* consists of β-Proteobacteria, γ-Proteobacteria, and Flavobacteria (Cooper and Cressler, 2020). However, individual zooplankton species can vary in their ability to host bacterial communities (Wang et al., 2021).

Biodetritus-bacterial microbiotic particles

In soil, bacterial aggregates can be established on biodetritus, which is physically unbound (not bound to soil mineral particles), particulated dead organic matter, including partially decomposed vegetables and animals (such as nematodes, entracheids, or pot worms) (Carter and Gregorich, 2007). Biodetritus is certainly not a part of the biota; however, its slow degradation and catabolism creates a dynamic structure somewhat analogous to the trophic-dynamic aspect of the biota, thereway influencing attached bacteria (Rich and Wetzel, 1978). In seawater, diatom detritus is heavily colonized by γ-*Proteobacteria*, α-*Proteobacteria* and *Flavobacteria* (Abell and Bowman, 2005). Phytoplankton bio-detritus creates a dynamic “detritosphere” with microbial processes of aggregation and degradation involving bacterial and protozoal successions (Biddanda and Pomeroy, 1988). Detritus originating from seaweeds and carrying attached bacteria, including *Proteobacteria, Bacteroidetes, Firmicutes, Cyanobacteria, Planctomycetes, Actinobacteria* and *Verrucomicrobia* might also play a role in the spread of microbiotic particles (Selvarajan et al., 2019). Certainly water-farming (as for salmon) create conditions favoring the production of microbiotic particles near the farming facilities (Poirier et al., 2020)

Humus-bacterial microbiotic particles

Humus is the organic dark material in the ground resulting from the decomposition of plant and animal matter. The humic material can be of colloidal size (humic and fulvic acids) or larger and insoluble (humins); this material degrades, eventually resulting in soluble compounds. Studies with atomic force microscopy characterized the interactions between natural organic material and bacteria; adhesion was proportional to the molecular weight of the material, the size of the particle, and its charge density. The charge of the bacterial surface also influences adhesion(Abu-Lail et al., 2007). Humus form flocculated complexes with clay particles (see below).

Mineral-bacterial microbiotic particles

Organo-mineral assemblages are micro-aggregates involving bacteria, which is facilitated by bacterial extracellular polymeric substances. Pre-existing soil aggregate bacterial communities are incorporated into water environments under circumstances of soil-water merging. However, most aggregate bacterial communities and therefore most microbiome interactions are established in small (less than 2 mm) soil mineral aggregates of heterogeneous origins (such as clay minerals, that is, layered aluminum silicates, or carbonates), which are extremely resilient to physical-mechanical disruptions and water effects and form “microbial villages” (Wilpiszeski et al., 2019). Most importantly, microbes contribute to mineral (such as clay, or carbonates) authigenesis, which is the process of *in situ* formation of mineral particles in sediments. The microbial exploitation of suspended clay particles in liquid environments promotes their micro-aggregation (Watts et al., 2005). Microbial biofilms constitute a reactive exopolysaccharide matrix that binds soluble chemical components and form solid inorganic particles (Konhauser and Urrutia, 1999; Wei et al., 2021). Structurally, the clay leaflets might be arranged in the form of 'houses of cards' and in fact aggregates look like 'hutches' housing the bacterial cells (Lünsdorf et al., 2000). Increased electrostatic interactions between clay particles, and the mineral-attached biofilm is critical for the flocculation process. forming bridges between clay particles, and leading to flocs formation (Mueller, 2015).

Anthropogenic litter and bacterial microbiotic particles

A characteristic example of anthropogenic litter are microplastic particles, which are millimeter-sized plastics, that can be currently detected in aquatic ecosystems worldwide. Many microbial organisms adhere to microplastics, forming biofilms (the microbial plastisphere) (Reisser et al., 2014; Galafassi et al., 2021). In Chinese river water, bacteria such as *Flavobacterium*, *Pseudomonas* (γ-Proteobacteria), *Rhodoferax* (β-Proteobacteria) *Janthinobacterium* (β-Proteobacteria) are enriched on microplastics when compared with water and sediment (Hu et al., 2021). The growing ensemble of microplastics in water probably constitute a novel ecological niche, exploited by bacterial biofilms hosting specific communities that differ from the surrounding planktonic ones (Sathicq et al., 2021).

Interactions among microbiotic particles in soil-water environments: bacterial coalescence and dispersal

All the previously considered microbiotic particles of various origins, can interact, aggregate, and eventually exchange microbial populations (Figure 1). The frequency of interactions is dependent both on the particle's local density and on the dynamics of the local environment (Rahlff et al., 2021). The natural or anthropogenic areas where soil and water coalesce (such as coastal waters, particularly those with significant tides, rivers and estuaries, the sea bottom, lakes and river beds, agricultural irrigation channels, mining and tunnelling water and mud flows, snow break streams, and waterfalls) constitute the main source of soil particles where bacteria find occasion for the establishment of compartmentalized biospaces (Figure 2). Such soil-water coalescence can be stimulated by occasional events, such as sea or river-originated floods, tsunamis and mud-tsunamis, accelerated deep sea currents, or heavy winds from terrestrial origin, including dust storms seeding from soil particles the sea surface movements (Behzad et al., 2018; Choufany et al., 2021; Pérez-Valdespino et al., 2021; Suhadolnik et al., 2021).

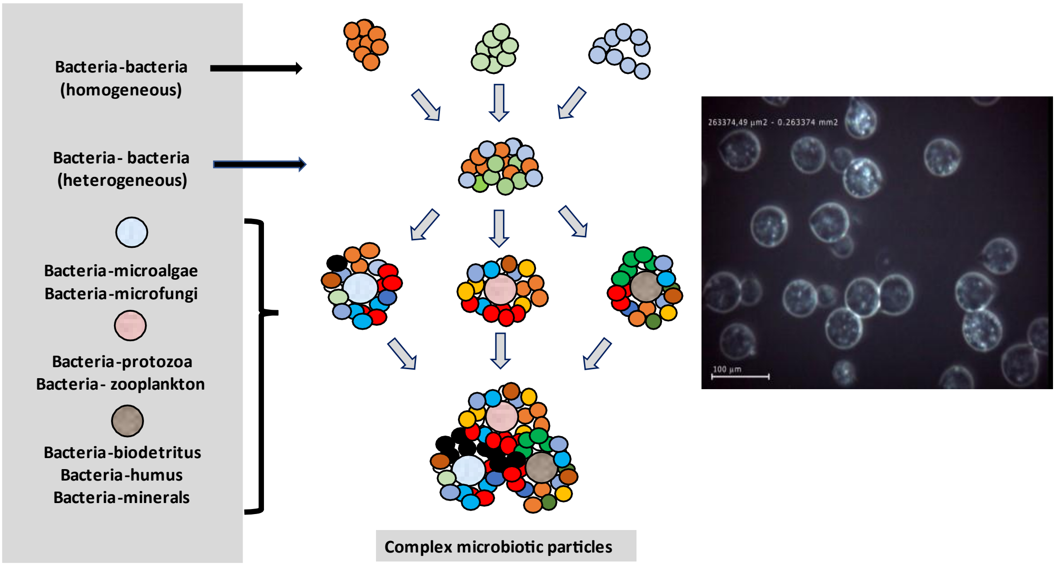

Figure 1. Formation of microbiotic particles. Inter-bacterial clumps are formed by aggregation of cells of the same population (homogeneous clumps) or coaggregation of cells from different species (heterogeneous clumps). Particles can be formed from

bacteria (or bacterial clumps) interaction in water and soil with microalgae, microfungi, protozoa, zooplankton, biodetritus, humus or mineral particles. Complex coaggregates result from merging of these particles. Balls of different colors represent different bacteria species or populations. The black ball is an antibiotic resistant bacterial population that might convert by genetic transfer other populations into antibiotic resistant ones (becoming black), which at they turn are able to make resistant their neighbors, eventually including pathogenic microorganisms. On the right side, alginate beads technology might be useful to trap, isolate, and study microbiotic particles of particular sizes.

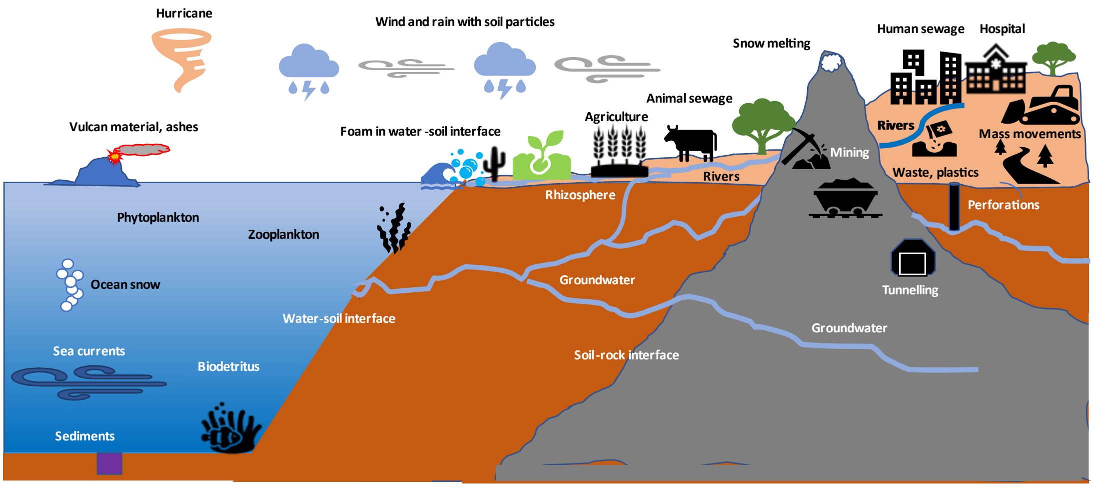

Figure 2. The origin and flow of microbiotic particles. Particles composed by, or aggregating bacterial populations, are generated in water and soil biological microparticles (including phytoplankton, zooplankton, soil particles, biodetritus) which coalesce in soil-water interfaces. Soil-water interactions among particles are favored by natural events (as floods, tsunamis, volcanic activity, raining, snow melting, sea, river

and groundwater dragging material, heavy winds) and those resulting from anthropogenic activities (human water waste, agriculture, farming, mining, tunnelling, mass movements in roads or urbanization activities). The coalescence of microbiotic particles from different origins favors heterogeneous bacterial coaggregation, resulting in possible genetic transfer of antibiotic resistance genes.

Natural landslides are a significant source of particles, including mobile intrusions produced by acute snow melt, intense rainfall, earthquakes, volcanic eruption, storm waves, rapid erosion from streams, and submarine landslides (Walker and Shiels, 2012). Microbial biodiversity in water is certainly increased by inoculation of microbes from soils (*Crump ISME*) In all cases, soil particles can mix with water during extended periods of time (mud formation), leading to increased microbial activity, reproduction and community mixing (Parvathi et al., 2019). Eruptions of muds and slurries (mud volcanoes) deeply influences bacterial and micro-eukaryotic communities (Coelho et al., 2016). Volcanic ash falling intp the sea supports a diverse bacterial community (Witt et al., 2017)

The role of anthropogenic soil-mass movements in the dispersal of bacterial-colonizable particles should not be underestimated, including agricultural and mining activities, urbanization, and parks or roads construction (Jaboyedoff et al., 2016). How climate change influences all these processes is an important issue. Warmer and drier periods retain soil microbioparticles that can then be dispersed by more frequent air and water runoff events (Fröhlich-Nowoisky et al., 2016). Air-carried particles are mostly from soil origin, and many contain microorganisms, forming the so-called “aerobiome” (de Groot et al., 2021). Microbes of such particles have a strong interaction with those of water bacterioneuston, bacteria located in the thin layer between water and air (Cunliffe et al., 2009; Hervas and Casamayor, 2009). particularly in foam interphases, favored by surface-active substances. Marine foam might contain a high abundance of γ-Proteobacteria including bacterioneuston organisms as *Pseudoalteromonas* and *Vibrio* (Rahlff et al., 2021).

Indeed, most particles of sufficient size ("large villages") have a stratified bacterial community structure, with deep, very stable residents, and more mobile (exchangeable) populations on the surface (Bailey et al., 2013). Such mobility is certainly reduced under dry conditions, and significant variations in moisture might periodically or intermittently occur. Not much is known about the consequences of the drying process, but in principle Gram positives should retain viability whereas Gram negatives, such as Enterobacterales, with a lower salt tolerance (Brown, 1976), will be submitted to water stress and can be reduced in number. However, some bacterial Gram-negative organisms have adapted to periodic water stress by excreting glycoproteins and polysaccharides. This adaptation is probably the main function of alginate, which can retain moisture and assuring viability of under dry conditions (Gacesa, 1998; Marshall et al., 2019). That results in the formation of a biofilm under which other coexisting bacteria might be spared from extinction. Alginate also provides osmotolerance, probably by intracellular accumulation (Sá et al., 2019). In addition, exopolysaccharides coating soil particles, and dead bacterial remains, contribute to the formation of aggregates where next incoming bacterial communities might attach (Kindler et al., 2006). Particular attention should be paid to predicting "microbial hotspots" in soil, where generally plant-associated microbiotic particles, can bloom in short periods of time (Kuzyakov and Blagodatskaya, 2015). These ephemeral hotspots also occurs in foamy particles in the sea surface (Rahlff et al., 2021).

It would be useful to construct a “grammar of interactions” among microbiotic particles, which should consider not only the identification of classic taxa, but the local ecotypes that help stabilize the diversification of the species to preserve the same functions despite environmental changes (García-García et al., 2019). Indeed that is influenced by the of particle’s connectivity, depending on dynamics of the different ecological sub-compartments; as an example, evolution (diversification) of *Shewanella* differs in the upper ocean to the abyssal zones (Tang et al., 2021).

Microbiotic particles dispersal by marine snow

In water systems, the cumulative process of the aggregation of microbiotic particles is depicted by macroscopic aggregates (from 0.5 mm to a few centimeters in diameter), also known as marine snow (or lake snow), which sink in water at variable speeds (Alldredge and Silver, 1988). Microbiotic particles in marine snow frequently include fungi (Bochdansky et al., 2017). In fact, marine snow is a complex microhabitat containing a diversity of bacterial lineages such *Planctomycetes*, *Firmicutes*, *Bacteroides*, and the α-, γ- δ-, and ε- classes of the phylum *Proteobacteria* (Rath et al., 1998). Such biological richness influences processes of microbial photosynthesis, decomposition, and nutrient regeneration, constituting a real snow microcosm (Azam and Long, 2001). Typically, microorganisms contained in marine snow are subjected to successional changes, derived from the earlier processes, eventually leading to disaggregation, and sinking kinetics (Alldredge et al., 1990). Bacterial successions can also be the result of specific amensalistic interactions mediated by antimicrobial substances (Grossart et al., 2003), as occurs in other natural microbiotas (Baquero et al., 2019). In addition to vertical migration of marine snow (Mestre et al., 2018; Sanz-Sáez et al., 2020), and suspended sediment aggregates, horizontal migration associated with currents and water flows (Simon et al., 2002), also occur, contributing to the dispersal of the composing microbiotic particles and the new possible associations with other microbial communities (Droppo, 2001). The final result is the dissemination of microorganisms to very distant environments (Hooper et al., 2008) (Figures 1 and 2).

Processes of micro and macro-aggregation determine the bacterial content of water sediments, and particularly of the benthic zone, where soil and water coalesce, a field that requires further research (Simon et al., 2002; Wotton, 2007). In fact, particle-attached bacterial communities in the deep ocean have a particular lifestyle as compared with free-living organisms (Acinas et al., 2021).

Evolution in the compartmentalized water biospaces

Several models have been established to study evolution in compartmentalized biospaces. A number of particulated biotic interactions tends to be fixed by evolution, such as algae-bacteria interactions (Ramanan et al., 2016). Experiments with artificial microcapsules, for made with a "membrane" of alginate-chitosan (Figure 1) have shown that compartmentalization in particles can contribute to the preservation of diversity (Zadorin et al., 2019), evading the dominance of a single organism or genotype resulting from periodic selection that occur in homogeneous environments (Atwood et al., 1951). Preservation of diversity in particles fosters genetic drift, and therefore maintains potentially adaptive changes that are lost in mixed planktonic environments (Baquero et al., 2021). In addition, particulation of communities ensures that different genotypes can be subjected to environmental stress, contributing to the overall evolvability of natural populations (Baquero, 2009; Rocca et al., 2019).

Bacterial populations tend to form closed compartments, such as colonies or biofilms attached to biotic or abiotic surfaces. There are probably "surface recognition" signals leading to these multicellular structures (Troselj et al., 2018; Kimkes and Heinemann, 2020). Such dense-population organizations have an internal structure with layers of cells in various physiological stages, “compartments within compartments” (You et al., 2019), and can release organisms outside the compartment, such it occurs when planktonic cells are released from sessile populations in biofilms (Bester et al., 2009). It has been proposed that evolution in biofilms generate greater genetic diversity than mixed planctonic environments, and this enhanced diversity leads to different pathways of antibiotic resistance (Santos-Lopez et al., 2019). In fact surface-microbe biology frequently leads to local differentiation, including the emergence of antibiotic resistant mutations (Rainey and Travisano, 1998; Oliver et al., 2000).

Compartments can be occupied by multiple species, and there are also multispecies biofilms in natural environments (Yang et al., 2011), frequently resulting from spontaneous coaggregation (Rickard et al., 2003). How densely populated compartments, such as biofilms can be invaded by external microorganisms (which can become part of the consortium) is an interesting topic that has been recently modeled, showing the importance of species concentrations on the biofilm free boundary ((D’acunto et al., 2014)) In any case, such dense aggregation of diverse populations facilitates horizontal gene transfer (including antibiotic resistance genes), and it has been proposed that biofilm communities in water environments are hot spots for gaining adaptive traits (Zadorin et al., 2019; Abe et al., 2020).

Particulation by microbial coaggregation: functional ensembles?

Coaggregation refers to a process by which individual microbial individual cells, either from a single clonal lineage or species, or from different species, recognize and attach to one another (London J et al., 1996; Rickard et al., 2003)The clues for recognition are not yet understood in detail, but most probably are the result of natural selection, and should involve a kind of surface recognition code, probably involving lectins and polysaccharide interactions, resembling the DNA codes used in protein synthesis (Baquero, 2014). Clumps or coaggregates involving two types of cells are formed immediately upon mixing the partner populations, a phenomenon that has been particularly studied in oral plaque microbial consortia (Kolenbrander et al., 1993)Various methods have been evaluated to measure coaggregation (Kinder and Holt, 1994). Quantitative spectrophotometry (based on flocculation of clumps) has shown that coaggregation occurs weakly among bacteria from different sites, such as oral or intestinal species (Ledder et al., 2008). A complete "grammar of interactions" is not yet available, but will be critical to understand the niche's coalescence and the resulting microbiome merging, which could be described as multidimensional network (Baquero et al., 2019, 2021). Some species serve as bridging "nodes" to which other species attach, as it has been shown with *Acinetobacter* species in water bodies, from activated sludge (Malik et al., 2003) to drinking water (Simões et al., 2008), or with *Blastomonas* in fresh water (Rickard et al., 2002; Afonso et al., 2021). Extracellular polymers play an important role in coaggregation of aquatic biofilms (Hede and Khandeparker, 2020). There is an "ecology of coaggregation", so that the process can be modified by variations in external physical or chemical factors (Oki et al., 2018). In general, however, coaggregation ensures the permanence (resilience) of species-species interactions in fluctuating environments.

Does a reproducible coaggregate act as a single individual biological unit? Are stable coaggregates endowed with particular organism-like traits? Certainly, there are chemical interactions among members of multispecies biofilms (Yang et al., 2011; Burmølle et al., 2014; Liu et al., 2016). It has been shown that gene expression in the partner species can be modified by coaggregation (Jakubovics et al., 2008), and therefore the coaggregate can be a source of emerging properties from a social individuality (Sadiq et al., 2021). The major difficulty in predicting the composition of microbiotic particles is due to the multi-stability in multispecies communities, combining with ecological noise (Wright et al., 2021).

Microbiotic aggregates and antimicrobial resistance

Both antibiotics and antibiotic resistance genes originate and are present in water and soil environments (Martínez, 2008; Cabello and Godfrey, 2018)In recent decades (1970 to the 2000s) the abundance of antibiotic resistance genes in European archive soils have increased 10-fold (Knapp et al., 2010). Microbiotic aggregates in soil and water environments have a considerable influence on the emergence and evolution of antimicrobial resistance (Baquero et al., 2021). There are several reasons:

1) Efficient antibiotic interactions require close cell-cell physical neighborhood (Burmølle et al., 2014), even cell-to-cell contact (Lemonnier et al., 2008).

2) Non-aggregated antibiotic-producers do not reach the critical density to ensure antibiosis, and non-aggregated susceptible organisms do not reach the number that ensures the acquisition of mutations or the acquisition of foreign resistance genes, which in some cases respond to quorum sensing.

3) Cell-to-cell contact is required for interbacterial horizontal gene transfer of antibiotic-resistance genes, and involves transformation, conjugation (plasmids, integrative-conjugative elements), and particularly in soils and marine habitats, DNA-packing extracellular vesicles and DNA transfer through intercellular nanotubes (Woegerbauer et al., 2020) .

4) “Functionally equivalent” bacterial species tends to cluster in the same type of aggregates, and kin-recognition favors the horizontal transfer of antibiotic resistance genes (Baquero et al., 2019). Most microbial organisms present in water and soil aggregates, including all branches of the Proteobacteria phylum (most antibiotic-resistant gram-negative pathogens belong to γ-Proteobacteria) can exchange genes, including antibiotic-resistance and metal-resistance (Kloesges et al., 2011; Pohl et al., 2014). Horizontal gene transfer is frequent in the oceans (McDaniel et al., 2010; Hemme et al., 2016).

5) Most organisms producing antibiotics have a soil or water origin. The genus S*treptomyces* (Actinobacteria in general) is one of the self-aggregated bacterial organisms more frequently found in soil and water. Interestingly, this class of organisms is the main source (at least two-thirds) of the groups of antibiotics used in the treatment of infections, including aminoglycosides, beta-lactams and beta-lactamase inhibitors, tetracyclines, macrolides, lincosamides, streptogramins, phenicols, rifamicins, fosfomycin, glycopeptides, novobiocin, daptomycin, or platensimycin, and these antibiotics are only the tip of iceberg of the detected antimicrobial compounds (Mast and Stegmann, 2019). Self-aggregation of dividing cells is probably an evolutionary strategy to produce locally sufficient concentrations of bioactive compounds, as antibiotics, either acting as antimicrobials or as intermicrobial signaling agents (Linares et al., 2006). In addition, there is always the possibility of transfer of antibiotic resistance genes from antibiotic producers to pathogens (Jiang et al., 2017). In water, organisms such as *Shewanella* are frequently part of coaggregates, and might be involved in the spread of antibiotic resistance (Rickard et al., 2003; Cabello and Godfrey, 2018).

6) Antimicrobials of anthropogenic origin are extensively polluting soil and water environments, and they tend to accumulate in particulated material (Baquero et al., 2008;

Rodriguez-Mozaz et al., 2020; Huang et al., 2021)retaining their antibacterial activities and consequently selecting, even at very low concentrations, for antibiotic resistant bacteria (Chander et al., 2005).

7) The most dangerous type of microbiotic particles involved in antibiotic resistance are those resulting from human and animal fecal pollution of water and soil, including those originating in waste water treatment plants (Karkman et al., 2018; Pärnänen et al., 2019). Large-scale wastewater treatment plants discharge hundreds of tons of total suspended particles into water bodies every year, and antibiotic resistance genes are perpetuated in the sediments (Brown et al., 2018). However, a significant decay of resistance genes can occur over time in some environments (Brown et al., 2020). Microbiotic particles based on microplastics contribute to the emergence and spread of antibiotic resistance (Wang et al., 2020; Hu et al., 2021). However, the relative importance of microplastic biotic particles is dependent on the inoculation environment and the weight of such contribution can differ by location (Galafassi et al., 2021).

The effect of antibiotic anthropogenic pollution has penetrated in the deepest region of the oceans, such as the Mariana Trench, where antibiotic resistance genes of possible human or animal origin have been detected (Yang et al., 2021). In fact, an ocean resistome, with an ensemble of antibiotic resistance genes, is now available, that includes genes conferring resistance to some of the most relevant clinical antibiotics, some of them which are particularly abundant in specific geographic locations (Cuadrat et al., 2020). Further research is needed to correlate these findings with the density of the various microbiotic particles.

Counteracting antibiotic resistance by controlling microbiotic particles

How can we counteract the dangerous spread of antibiotic resistance mediated by water-soil particles? It appears to be an almost impossible task at the global scale, but eventually some interventions can be locally effective. Note that density and distribution of particles might bias surveillance results focusing bacterial fecal pollution. The density of suspended particulate matter influences the recovery of faecal indicator bacteria, and this “local factor” should be taken into account (Perkins et al., 2016). Access to water bodies of human and animal microbiotic particles containing antibiotic resistance is highly dependent on the socio-economic status of the country, and this access, based on a lack of proper sanitation procedures, is probably more important than the antibiotic consumption in shaping the local rate of resistance in human and animal pathogens(Collignon et al., 2018).

Removal of water microbiotic particles is an essential step to decontaminating the environment from antibiotic resistance (Kumar and Pal, 2018; Liang et al., 2021). Various procedures have been proposed (Lawler, 1986) or are under research for removal or deactivation of water particles. In addition to the classic sedimentation, flocculation, coagulation, or disinfection process, filtration and ultrafiltration, as well as cold atmospheric plasma technology (Kim and Dempsey, 2008), hydrodynamic vortex separators (Gronowska-Szneler and Sawicki, 2014); dissolved air flotation (Han et al., 2007; El-Kalliny et al., 2021) and other procedures will be necessary. Nanoparticles-based biotechnology is a promising field. The field includes “insertion” in the natural process of aggregation of nanoparticles that recognize particular microorganisms (even located in biofilms) and kill them, such as those synthesized from natural organic matter (mostly composed of humic and fulvic acids) and silver or gold particles, which are then released in the environment. The use of nanoparticles with zinc oxide and titanium dioxide in combination with halophilic bacteria (which reduce nutrients) has been proposed to reduce the biological part of microbiotic particles (Weber et al., 2021). However, the environmental safety of nanoparticles remain in discussion (Hajipour et al., 2021). Other suggested approaches is the use of “environmental probiotics” as *Pseudoalteromonas,* with antibiofilm activity (Dheilly et al., 2010) or particular types of natural clay minerals with antimicrobial and antibiofilm effects (Behroozian et al., 2020)

Final coda: microbiotic particles in planetary health

The preservation of a healthy equilibrium among biological and chemical constituents of the human-colonized Earth constitutes the objective of the One Health and Global Health approaches, in fact, of Planetary Health (Myers, 2017; Hernando-Amado et al., 2019). Such equilibrium can be altered by human interventions, as can be depicted by the deleterious changes in the oceans (Pedrós-Alió et al., 2021), and it requires robust counter-interventions to ensure that Earth’s organisms are maintained in a homeostatic, constant internal state despite perturbations from their surroundings (Tang and Mcmillen, 2016). From a Planetary Health perspective, we can propose that the dynamic network of interactions among microbiotic particles in the soil and water constitute a linking material, a kind of cement for a unified life-holobiont, where everything depends on everything else (Davies, 2009). The analysis and characterization of such a network requires further research, which should lead to suitable corrective interventions to ensure our common well-being.

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