The Thematic Fields of Microbial Ecology

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Abstract

The microbial world, generally invisible to the naked eye, has largely shaped our environment and has been instrumental in the emergence and evolution of all other living organisms on Earth. These microscopic unicellular organisms were for 3 billion years the only forms of life on our planet.

Their most spectacular action was the modification of the primitive atmosphere: the dioxygen certainly not present initially reached its present concentration (21 % of the gas content of the atmosphere) through the action of microorganisms that are able of oxygenic photosynthesis. For the evolution of life, it is now widely accepted that multicellular life forms extremely complex have emerged from eukaryote microorganisms classified in the kingdom Plantae and in the Stramenopiles and Opisthokonta (especially metazoans which includes humans). These life forms are still dependent on the activity of microorganisms.

If a disaster, whether natural or caused by humans, should annihilate all nonmicrobial living species, it is likely that some microorganisms that have colonized all oceans (from the surface to the abyssal domain) and the earth's crust (to a depth of hundreds of meters) would be spared and would allow the initiation of a new evolution process, whatever the new environmental conditions at the end of this disaster, except in the absence of liquid water.

Keywords

Biogeochemical cycle • Distribution • Diversity • Ecosystems • Evolution • Interactions • Origin • Taxonomy • Xenobiotics

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Their most spectacular action was the modification of the primitive atmosphere: the dioxygen certainly not present initially reached its present concentration (21 % of the gas content of the atmosphere) through the action of microorganisms that are able of oxygenic photosynthesis. For the evolution of life, it is now widely accepted that extremely complex multicellular life forms have emerged from eukaryote microorganisms classified in the kingdom *Plantae* and in the Stramenopiles and Opisthokonta (especially metazoans which includes humans). These life forms are still dependent on the activity of microorganisms.

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The activity of the biosphere as a whole is totally dependent on the action of microorganisms. The major goal of microbial ecology (which, in general, can be defined as the study of microorganisms in natural and anthropized ecosystems) is to improve our understanding of:

1. *Their origin and evolution*

   The first inhabitants of the Earth, microorganisms have developed mechanisms that allowed them to adapt to all climatic and geological changes that have occurred on the Earth since the origin of life. They are actually present in all habitats and are able to adapt to the most extreme conditions of life in terms of temperature, pressure, pH, salinity, radiation, etc.

   To explain the longevity and ubiquity of microorganisms, it is important to take into account the very short duration of their cell cycle, their high mutation rates and adaptability to environmental changes, their extraordinary metabolic plasticity that allows them to adapt to a large diversity of carbon and energy sources that are available in their environment (including xenobiotics, which are molecules produced by humans), the diversity as well as the frequency of genetic information transfer between populations and communities, and their ability to survive under starvation conditions and all resistance strategies to face environmental stresses. This resistance can involve morphological and metabolic changes such as the production of detoxifying enzymes, DNA repair mechanisms, and the production of resistance forms (endospores, cysts, etc.). In addition, their small size results in a very high surface/volume ratio and therefore in a high exchange capacity with the external environment. This capacity promotes their ubiquity in natural environments (Woese 1987).

2. *Their taxonomic and functional diversities and their abundance and distribution in ecosystems*

   The microbial ecologist is led to inventory microorganisms in the environment, which means all prokaryotic and eukaryotic unicellular microorganisms but also viruses in their functional dimension. The microbial compartment is a component of all ecosystems, similar to the animal or plant components. In addition to this taxonomic diversity, microbial ecologists have to describe the functions that microorganisms are in charge of, which means understanding which genes are involved and expressed in situ (Brock 1966).

3. *Their role in the functioning of ecosystems and in particular that of biogeochemical cycles*

   Due to their important biomass, metabolic diversity, and capacity to adapt to the environment, microorganisms play a major role in the organization, functioning, and evolution of ecosystems. They are both producers, consumers, and decomposers, and they participate in all stages of the organic and mineral matter transformation, and they are alone to perform some transformation processes. Their role is also essential in the functioning of food webs. In the absence of plants and animals, biogeochemical cycles could continue to operate based solely on the activity of microorganisms. The study of their role in the different cycles requires the description, location, and quantification of microbial populations and communities that are involved, as well as the characterization of all organic matter degradation and synthesis pathways and the measurement of their activities. On this last point, it is important to note that if the action of microorganisms proceed at the microenvironment scale, the impact of their activities apply at the earth scale (Fenchel et al. 2000).

4. *The interactions between microorganisms and between microorganisms and plants, animals and humans*

   All together, these interactions which are in most cases positive (beneficial) or negative (adverse) are classified as biotic interactions. In the environment, microorganisms do not live alone: they form populations often grouped into communities and can form highly structured assemblages such as biofilms or microbial mats. From the first stages of life, microorganisms have assembled to form multilayer structures called stromatolites which are microbial mats made with autotrophic and heterotrophic prokaryotes and fossilized for millions of years. The success of these associations is quite exceptional: if they have appeared more than 3 billion years ago, the stromatolites are still present. Studies of biotic interactions must take into account not only the interactions between microorganisms but also their interactions with multicellular organisms such as plants, animals, and humans (Margulis 1981).

5. *Interactions between microorganisms and their environment, considered as abiotic interactions*

Studies of these abiotic interactions should consider, on the one hand, how both physical and chemical properties of the environment may affect the presence, spatial distribution, and also the growth and activity of microorganisms and, on the other hand, the feedback of microorganisms on their environment. Among the environmental parameters interacting with microorganisms, the most important are pH, pressure, light intensity and wavelength, and the electron donor and acceptor concentration. These donors and acceptors are most often heterogeneously distributed in the natural environment and/or present at low concentration. As a consequence, they do not allow the maximum development of microorganisms and their survival under environmental conditions that are not adapted to their physiology. In most environments, microorganisms are most often living under nutrient starvation, leading to long periods of dormancy. They adapt to these starvation conditions by developing nutrient storage systems or other mechanisms (chemotactic, phototactic, magnetotactic) enabling them an easier access to nutrients. More generally, microorganisms must continuously adapt to survive to regular and sometimes fast changes of the environmental parameters.

The interaction of microorganisms with natural surfaces (soil or sediment particles, leaves and roots, digestive tract of humans and animals, skin, etc.) must also be considered. In the natural environment, many microorganisms are not free-living organisms, but they attach to most surfaces through the secretion of extracellular compounds such as polysaccharides that allow them to form biofilms or microbial mats (Fenchel et al. 2000).

6. *Their extraordinary capacity to degrade pollutants, especially xenobiotics, as a service to ecosystems and to the bioremediation of contaminated sites*

Microbial ecology can provide solutions to many environmental problems currently faced by human societies whose relationships with the environment have changed dramatically during the last centuries due to an important increase of the world population, to the settlement of populations over an extended range of biotopes, and more recently to the industrial development and, therefore, to the production of more and more domestic and industrial wastes, leading to an increasing pollution of environmental sites. Nowadays, pollution has reached such levels that it endangers the survival of a large number of species on Earth. An important goal in microbial ecology is to enhance the metabolic properties of microorganisms to degrade most pollutants that affect our planet. Microbial ecology is also concerned by public health problems such as an increasing need to produce drinking water, food contamination, dispersion, and changes in the behavior of pathogens in the environment (emerging infectious diseases, viable but nonculturable state of pathogens, antibiotics resistance, etc.).

These are the objectives of microbial ecology, at the interface between microbiology and ecology. To achieve these goals, it is important to develop appropriate and efficient methods, sometimes specific to the study of microorganisms in natural environments. In this matter, real-time methods are more and more requested to develop early warning detection systems. Sergei Winogradsky, the first microbiologist that has introduced the expression "environmental microbiology," pointed out the limitations and drawbacks of the methods that are commonly used in medical and industrial microbiology. Based on the study of microorganisms that have been isolated and grown under controlled conditions, most of these methods cannot be used to investigate the life and physiology of environmental microorganisms. This vision was especially appropriate since it is now well established that many microorganisms that are present in the environment are unknown and only 1–10 % of microbes present in natural biotopes have been grown in pure culture (Singh 2011).

Techniques have been developed that allow a direct access (without any cultivation step) to microbial populations and communities in the environment thanks to the increased performances of microscopy instruments and analytical chemistry techniques (development of fluorescence techniques and **biomarkers***, identification of metabolic pathways), development of microelectrodes to assess the distribution and activity of microorganisms at the microscale, use of isotopic techniques, development of techniques to determine the activity of microorganisms under conditions very close to those encountered in the natural environment (e.g., hyperbaric instruments that generate high pressure, temperature, and oligotrophic conditions that exist in the deep ocean, etc.), and development and improvement of flow cytometry instruments to access the properties of individual cells (numbers, physiological state, presence or absence of certain metabolic activities, etc.).

Nevertheless, the main technological revolution in this field was the implementation, development, and use of molecular biology techniques: DNA fingerprinting, DNA chips (taxonomic and functional), metagenomic libraries, transcriptomic and proteomic studies, full genome sequencing, etc. Environmental genomics has allowed the detection, identification, and quantification of microorganisms in the natural environment after DNA extraction, with access to non-cultivable species. They also provided access to the physiological state of cells and were a considerable contribution to our knowledge of the diversity of microorganisms (taxonomic, functional, and genetic diversity), their phylogeny, activities, and interactions.

This book aims to address all issues related to this discipline. It consists of 19 chapters that are organized into 5 parts.

– The first part is devoted to "General Chapters." After an introduction (Chap. 1, "The Thematic Fields of Microbial Ecology"), the next chapters present a brief history of the discipline, including an introduction to the work of Winogradsky (Chap. 2, "Some Historical Elements of

Microbial Ecology") and a description of the structure and microbial metabolisms (Chap. 3 "Structure and Functions of Microorganisms; Production and Use of Material and Energy"). Indeed, understanding the role of microorganisms in the environment requires that their metabolism be known to understand their action in the transformation of organic and inorganic compounds within biogeochemical cycles or wastewater treatment processes (catabolism pathways, energy metabolism), as well as their action in interactions and food webs (anabolism pathways, biosynthesis). The remarkable metabolic diversity of prokaryotes, which is developed in this chapter (different aerobic and anaerobic respirations, fermentations, and photosynthesis), has allowed them to colonize and to be very active in all habitats of our planet and perhaps other planets.

– The second part "Taxonomy and Evolution" starts with a chapter entitled "For Three Billion Years, Microorganisms Were the Only Inhabitants of the Earth" (Chap. 4), where a description is presented of the last universal common ancestor (LUCA), different hypotheses of the emergence of three kingdoms that make up the living world today (Bacteria, Archaea, Eukarya), and the main stages of the evolution of microorganisms, in particular the main evolutionary scenarios that can explain the emergence of eukaryotic organization.

Chapter 5, "Systematic and Evolution of Microorganisms: General Concepts" presents general concepts related to this topic. In eukaryotes, it addresses primary endosymbioses at the origin of mitochondria and chloroplasts (in the kingdom of plants) and perhaps of the kinetic processes and secondary and tertiary endosymbioses causing photosynthesis in other eukaryotic kingdoms.

The "Taxonomy and Phylogeny of Prokaryotes" are presented in Chap. 6. The description of criteria used for phenotypic and genotypic characterization leads to a discussion of the problems associated to the definition of species in prokaryotes. The characteristics of the two prokaryotic kingdoms Bacteria and Archaea are defined. The current phylogeny of their major taxa is also presented.

Chapter 7, entitled "Taxonomy and Phylogeny of Unicellular Eukaryotes," suggests a unified terminology for the description of the cytology, morphology, reproduction, and biological cycles of eukaryotes. Major taxa of unicellular eukaryotes are presented with a focus on specific biochemical and cytological markers for each of them. Their position in the eukaryotic phylogenetic tree is specified.

– The third part "Microbial Habitats: Diversity, Adaptation, and Interactions" focuses on the study of "Biodiversity and Microbial Ecosystems Functioning" (Chap. 8).

Microbial biodiversity is a concept that emerged a few years ago to identify all the players in the microbial biotopes. This concept is first discussed in a historical perspective in relation to the paradigms in ecology. Then, mathematical approaches that are used to characterize all microbial actors are presented as well as the technical tools developed to quantify microbial biodiversity. Approaches to explore the relationship between biodiversity and taxonomic functional biodiversity are described for major ecosystems (soil, water, etc.) and the main functions (respiration, photosynthesis, fixation, and use of nitrogen). Finally, in the conclusion, there is a discussion of the prospects offered by the tools under development.

Chapter 9, "Adaptations of Prokaryotes to Their Biotopes and to Physicochemical Conditions in Natural or Anthropized Environments," concerns the adaptive processes developed by prokaryotic cells (two components regulatory systems, chemotaxis, etc.) and their metabolic and genetic responses to adapt to physicochemical conditions prevailing in the terrestrial and aquatic habitats.

Chapter 10, "The Extreme Conditions of Life on the Planet and Exobiology," deals with the microbial life in ecosystems of the planet that are characterized by extreme physicochemical conditions. In the first part, the great diversity of prokaryotes is described that colonize such environments, which were most often seen in the past as hostile to life. The ecological, physiological, and taxonomic properties of these indigenous extremophiles microorganisms are then exposed with particular emphasis on psychrophilic, thermophilic, acidophilic, alkalophilic, halophilic, and piezophilic microorganisms.

Chapter 11, "Microorganisms and Biotic Interactions," describes the interactions (cooperation, commensalism, competition, mutualism or symbiosis, parasitism, predation) involving microorganisms and their significance in microbe/microbe, microorganism/plant, and microorganism/animal or man interactions. It describes molecular and evolutionary mechanisms of bipartite and/or multi-interactions. The biological functions involved in these interactions are addressed in terms of impact on matter and energy fluxes in the environment, biotechnology, agronomy, and public health.

Chapter 12, "Horizontal Gene Transfer in Microbial Ecosystems," describes general features of horizontal gene transfer (HGT) (mechanisms, discovery, etc.). HGT are discussed from a qualitative point of view in relation to the adaptive response of microorganisms in the environmental conditions but also from a quantitative point of view, as a major evolutionary mechanism in microorganisms.

– The fourth part, "Role and Functioning of Microbial Ecosystems," discusses the intervention of microorganisms in "Microbial Food Webs in Aquatic and Terrestrial Ecosystems" (Chap. 13). The organisms involved in microbial food webs (MFWs), including viruses, Archaea, Bacteria, and many eukaryotic taxa

(Fungi, Alveolates, Mycetobiontes, etc.), play an essential role in the functioning of aquatic and terrestrial ecosystems. From this point of view, pelagic aquatic ecosystems are particularly original since primary production is only due to microbial communities who provide most of the biomass in these ecosystems. After an overview of MFWs and their main players, the various bottom-up (resources) and top-down (predators) factors controlling microorganisms are presented. Differences and similarities between aquatic and terrestrial MFWs are described.

Chapter 14, "Biogeochemical Cycles," concerns the role of microorganisms in the functioning of natural and anthropogenic ecosystems by studying detailed processes and mechanisms that are involved in the main biogeochemical cycles (carbon, nitrogen, sulfur, phosphorus, silicate, metals), in soils and in freshwater and marine ecosystems. The exchanges and biotransformations of organic and mineral components between the oxic and anoxic zones of the different biotopes are presented.

Chapter 15 presents "Environmental and Human Pathogenic Microorganisms" involved in humans or animal diseases through a large diversity of infectious mechanisms. The diversity of these pathogenic microorganisms, their mode of infection, and dissemination but also their behavior in the environment as well as the specific methods used for their detection are reported.

"Applied Microbial Ecology and Bioremediation" (Chap. 16) concerns the use microorganisms for preventive remediation (wastewater treatment plants, treatment of gaseous effluents) or bioremediation in contaminated sites (bioaugmentation, biostimulation, rhizostimulation, bioleaching). Most of the processes used to recover contaminated soils, sediments, and coastal effluents of treatment plants are reported. An important part of this chapter is devoted to the description of main pollutants in the environment as well as natural attenuation processes due to microbial activities (biodegradation and/or biotransformation).

– The fifth part "Tools the Microbial Ecology" describes the "Methods to Study Microorganisms in the Environment" (Chap. 17): sampling, microbial biomass and activity measurements, structure and diversity of microbial populations, and communities using cultural and noncultural techniques and laboratory studies. These methods are described for different types of microorganisms (prokaryotes and eukaryotes, heterotrophs and autotrophs) and different types of biotopes (water, soil, sediment, biofilms, etc.) providing informations on their advantages and limitations and using varied approaches and instruments such as cytometry, molecular biology, biochemistry, and isotopic and molecular electrochemistry.

Chapter 18 focuses on "Contributions of Genomics and Proteomics in Microbial Ecology" for studying the organization and functioning of complex microbial communities as a whole. Genomics and related methods (transcriptomics, proteomics, metabolomics) are addressed from historical and technical points of view. Some examples of the contribution of these techniques to the knowledge on microorganisms are reported, addressing their physiology and ecology in different environments.

Actually, the growing interest in microbial ecology also requires the quantification of microbial activities and biotic and abiotic interactions.

Chapter 19 on "The Modeling Microbial Ecology" aims to provide informations on the development of models in various fields of microbial ecology through some examples but also to highlight the current limitations of modeling in this field. The second objective of this chapter is to provide the reader the necessary bases to understand the scientific literature related to microbial ecology and for which mathematical modeling should be seen as a tool that complements more traditional methods of investigation (molecular biology, culture, genomics, etc.).

At the end of each chapter, a list of references including general books and major articles related to the different topics may help the reader to complete the scientific information presented in the chapter. Words in bold with an asterisk in the text are defined in a glossary at the end of the book, before the index.

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