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Review

Microbial mat ecosystems: Structure types, functional diversity, and biotechnological application

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ABSTRACT

Microbial mats are horizontally stratified microbial communities, exhibiting a structure defined by physiochemical gradients, which models microbial diversity, physiological activities, and their dynamics as a whole system. These ecosystems are commonly associated with aquatic habitats, including hot springs, hypersaline ponds, and intertidal coastal zones and oligotrophic environments, all of them harbour phototrophic mats and other environments such as acidic hot springs or acid mine drainage harbour non-photosynthetic mats. This review analyses the complex structure, diversity, and interactions between the microorganisms that form the framework of different types of microbial mats located around the globe. Furthermore, the many tools that allow studying microbial mats in depth and their potential biotechnological applications are discussed.

Contents

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1. Introduction

In nature, microorganisms often form communities adhering to a solid surface to form complex ecological assemblages in different habitats around the world [1,2]. Adherence to a surface is a strategy used for millions of years by microorganisms to survive and evolve in community and allows microorganisms to cope with the various abiotic factors that surround them, with some of them being stressful. These types of biological organizations range from simple monospecific biofilms to complex microbial mats formed by a wide variety of microorganisms, wherein a wide variety of ecological interactions are observed [3].

Microbial mats are benthic, vertically layered, and self-sustaining communities that develop in the liquid–solid interface of various environments [4]. Furthermore, they comprise millions of microorganisms belonging to different species, which interact and exchange signals, embedded in a matrix of exopolysaccharides, and nutrients to enable a greater flow of resources and energy for the survival of the community [5]. The associations observed are restricted, with some of them being symbiotic, which confers them a selective advantage [6,7].

Microbial mats have been present on Earth for millions of years, the oldest of which are found in sedimentary rocks of 3.7 Ga and 3.4 Ga west of Australia [7,8,9,10,11] and South Africa [12], respectively, from the Archaean era. However, it was present in a greater abundance in the Proterozoic (2.5–0.57 Ga) era, with worldwide distribution [13]. The extensive fossil record suggests that these communities are highly stable and flexible in adapting to continuous environmental changes [13]; these ecological assemblages today persist in extreme environments such as hypersaline ponds, hot springs, and sulfur springs, where environmental conditions restrict and limit the growth of some multicellular and eukaryotic organisms [14,15].

The role of microbial mats has been crucial throughout the history of the Earth for the composition and modification of the atmosphere, producing O_2, H_2, and CH_4 [16] and also represents the first ecosystems together with stromatolites. Thus, microbial mats are, undoubtedly, a natural laboratory where microbial diversity (patterns and community structure), evolutionary processes, and their adaptation to extreme environments can be studied [17,18,19]. In this review, we analyze in detail the complex structures that comprise a microbial mat, the different types of microbial mats, and their microbial diversity. Furthermore, we have analyzed the main tools, including a perspective on its potential application in areas such as medicine, different industries, and bioremediation of contamination due to luminaires used for studying microbial mats in the last decade.

2. Structure, functionality and ecological dynamics of microbial mats

Microbial mats are structures visible to the naked eye, with the thickness ranging from millimeters to several centimeters, and are formed by multiple biofilms of microorganisms embedded in a matrix of exopolysaccharides [20] in a vertical fashion due to the physical gradients (Fig. 1) [21]. One of the main factors of biological diversity in microbial mats is attributed to its dynamic physiochemical gradients, which are largely modified by the biological processes of the inhabiting microorganisms. These biological processes and physical gradients provide the required microenvironments and ecological niches for microorganisms with specific needs [4,7,22]. These communities are essentially formed by organisms of the domain 'Bacteria'; however, the domains 'Archaea' and 'Eukarya' are also involved in forming microbial mats, although less diverse and abundant in nature [23].

The chemical parameters to be considered for studying microbial mats are the presence of oxygen, pH, redox potential, saline concentration, presence of electron donor and acceptor compounds, and the diversity of chemical species, whereas the important physical parameters to be considered include light, temperature, and pressure. The study of biological interactions (symbiotic, neutralism and amensalism) in the mats is another relevant aspect that we have considered in this review [24]. Relevant processes such as photosynthesis, nitrogen fixation, denitrification, metal reduction, sulfate reduction, and methanogenesis are vital to the performance of mats [25,26].

Microbial mats consist of various basic biofunctional groups such as Cyanobacteria, anoxygenic photosynthetic bacteria (generally represented by non-sulfur green bacteria of the Chloroflexi division), green sulfur bacteria (Chlorobi) and purple bacteria (Proteobacteria division), aerobic heterotrophs and anaerobes, sulfate-reducing bacteria (SRB), sulfur oxidizing bacteria and methanogenic archaea [22,27].

The main source of energy and nutrition of microbial mats is through photosynthesis [7], although non-photosynthetic mats exist. In a typical mat, the first step for survival of this trophic network is photosynthesis, a process in which light energy is utilized to fix inorganic carbon (CO_2) to organic carbon ($(CH_2O)_n$), thereby releasing oxygen (Fig. 2), performed by the primary producers Cyanobacteria [28,29]. Microbial mats function as a consortium where biogeochemical cycles and biochemical processes are coupled [30], and this close interaction allows the products of the metabolism of one group to be available and used by other microorganisms.

Nitrogen fixation is primarily performed by unicellular and filamentous Cyanobacteria; however, SRB have been found to play a key role in this biological process [31]. SRB are an important group of bacteria capable of reducing sulfates to sulfur, oxidizing organic matter, and obtaining energy in the process. In addition, SRB are essential for calcium precipitation and lithification of mats, and therefore, are responsible for mat preservation in fossil record [28].

The formation of these complex communities is performed by a process of ecological succession, wherein the Cyanobacteria are the colonizing organisms and microenvironment modifiers for the later colonization of more specialized bacteria and with higher and specific environmental requirements [32]. In addition, a microbial mat is a dynamic community in which microorganisms are capable of motility

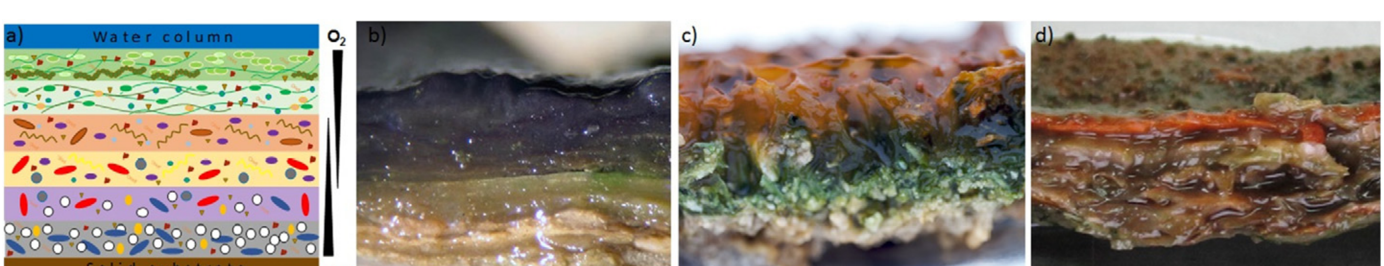

Fig. 1. General structures of microbial mats. The thickness can range from millimeters to several centimeters, and are formed by multiple biofilms of microorganisms embedded in a matrix of exopolysaccharides, in a vertical fashion due to the physical gradients.