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REVIEW

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Geoarchaeological microbiomes and artifact preservation: a review

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ABSTRACT

Microbiomes play a dual role in the preservation and degradation of archaeological artifacts. Certain microbial communities, such as Aspergillus, Cladosporium, and Pseudomonas, contribute to biodeterioration through acid production, enzymatic degradation, and biofilm formation. Conversely, species like Bacillus and Actinobacteria facilitate preservation via biomineralization and microbially induced calcite precipitation (MICP), reinforcing structural integrity. Recent advancements in metagenomics and proteomics have improved the characterization of microbial communities in heritage sites. However, challenges persist in distinguishing beneficial from harmful microbiota and understanding their long-term ecological dynamics. While biofilms contribute to biodeterioration in sites such as Lascaux Cave, controlled microbial biofilms have been successfully applied in the Roman Catacombs to protect surfaces. Genetic engineering, including CRISPR-based modifications, holds potential for conservation but remains in its early stages of application. Digital heritage technologies, such as 3D scanning, Raman spectroscopy, and Fourier-transform infrared (FTIR) spectroscopy, provide non-invasive means to analyze microbial colonization patterns and biodeterioration processes. These approaches enable real-time monitoring and evidence-based conservation strategies. Sustainable microbiome-based conservation efforts, such as bio mineralization using Bacillus spp., have been implemented at Angkor Wat, demonstrating microbial interventions' efficacy in stabilizing heritage structures. This review explores the role of geoarchaeological microbiomes in artifact preservation and deterioration, highlighting the mechanisms through which microorganisms influence cultural heritage materials. By synthesizing current research on microbial interactions, conservation challenges, and technological advancements, it aims to provide insights into sustainable preservation approaches.

KEYWORDS

Microbiomes; Enzymatic degradation; Biofilm formation; Lascaux cave; Roman Catacombs

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Introduction

Microorganisms are fundamental to Earth's ecosystems, driving processes such as nutrient cycling, such as nitrogen fixation, and organic matter decomposition. In archaeological contexts, microbial communities or microbiomes interact with artifacts, monuments, and historical structures, influencing their preservation and deterioration [1]. The study of these interactions has led to the emergence of geoarchaeological microbiomes, a field dedicated to understanding microbial communities present in archaeological soils, artifacts, and built heritage [2].

Geoarchaeological microbiomes consist of diverse microbial populations found in archaeological matrices, including soil, stone, wood, and metal artifacts. The microbial composition varies among these matrices, with stone surfaces harbouring biofilm-forming cyanobacteria, while metal artifacts are often colonized by sulfate-reducing bacteria that accelerate corrosion [3]. These microorganisms play a dual role: while some contribute to biodeterioration, leading to material degradation through acid production, biofilm formation, and corrosion, others facilitate preservation through biomineralization, biofilm stabilization, or microbial-induced calcite precipitation. Understanding these microbial interactions is crucial for developing conservation strategies that mitigate damage while harnessing protective microbial functions [3,4].

Recent studies underscore the significant impact of microbial activity on cultural heritage. For example, in the Mayan historical monuments of the Yucatán Peninsula, microbial colonization has contributed to stone surface degradation [5]. Conversely, some microbial communities aid in stone preservation via biocalcification and extracellular polymeric substance (EPS) biostabilization, a process in which microbial secretions form protective biofilms that stabilize the surface. The application of molecular techniques like metagenomics and proteomics has advanced the characterization of these microbiomes, offering insights into their functional potential in heritage conservation [6].

Despite advancements, challenges remain in fully deciphering microbial interactions with cultural artifacts. The ecological dynamics of microbial communities at heritage sites are not well understood, and the long-term effects of microbial activity on preservation remain uncertain. Additionally, difficulties in distinguishing harmful from beneficial microbial species complicate conservation efforts, particularly in long-term monitoring and intervention strategies [7].

This review explores the role of geoarchaeological microbiomes in artifact preservation and degradation, their interactions with archaeological sites, and recent advancements in heritage microbiome research. By synthesizing current

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knowledge, it aims to support evidence-based conservation strategies that leverage microbial processes for the protection of cultural heritage, with an emphasis on applying microbiome-based interventions for sustainable preservation.

Role of Microbiomes in Archaeological Sites

Microorganisms play a pivotal role in the preservation and degradation of archaeological artifacts. Their interactions with materials such as metals, stones, and organic compounds can lead to either deterioration or protection, depending on the microbial species and environmental conditions. Notably, sites like the Lascaux Cave in France have faced severe microbial-driven degradation, while Ajanta Caves in India have shown instances where biofilms have contributed to both preservation and deterioration [8].

Microbial interactions with artifacts

Degradation: Certain microbes contribute to the deterioration of artifacts through various mechanisms:

Acid production

Microorganisms such as fungi and bacteria can produce organic acids that corrode materials like stone and metal. For instance, Aspergillus niger secretes citric acid, leading to the solubilization of mineral components in calcareous stones, thereby accelerating decay [9].

Enzymatic activity

Hydrolytic enzymes produced by microbes can degrade organic materials. Fungi producing cellulase, amylase, gelatinase, and pectinase are highly active in the biodegradation of cultural heritage materials. Notably, in Egyptian tombs, fungal enzymatic degradation has led to visible damage on ancient mural paintings [10].

Biofilm formation

Microbial biofilms, comprising communities of bacteria and fungi, adhere to artifact surfaces, trapping moisture and promoting physical and chemical deterioration. The Lascaux Cave has experienced fungal biofilm formation, resulting in pigment discoloration [11].

Preservation: Conversely, certain microbial activities can contribute to the preservation of artifacts:

Biomineralization

Some bacteria induce the precipitation of minerals, forming protective layers on artifact surfaces. For example, Bacillus species can precipitate calcium carbonate, creating a protective crust over stone artifacts. A case study from Angkor Wat revealed that certain Bacillus strains contributed to the structural stability of stone monuments [12].

Protective biofilms

Beneficial microbial biofilms can act as barriers against environmental factors, reducing the impact of moisture and pollutants. Controlled biofilm applications have been explored in Italy's Roman Catacombs, where selected microbial communities were used to limit biodeterioration [13].

Microbial species involved in preservation

Several microbial taxa are notable for their roles in the preservation of cultural heritage materials:

Actinobacteria

Known for their ability to produce antimicrobial compounds, they can inhibit the growth of detrimental microbes on artifacts.

Pseudomonas spp.

Certain strains have been associated with the formation of stable biofilms that protect surfaces from environmental degradation.

Bacillus spp.

These bacteria are capable of inducing biomineralization processes, leading to the formation of protective mineral layers on artifacts [14].

Factors influencing microbial communities

The composition and activity of microbial communities in archaeological contexts are influenced by various environmental factors:

Soil composition and pH

The chemical makeup and acidity or alkalinity of the soil significantly affects microbial diversity and activity. Soils rich in organic matter support diverse microbial populations, while pH influences the solubility of nutrients and the viability of different microbial taxa [15].

Humidity and climate

Moisture levels and climatic conditions are critical determinants of microbial growth. High humidity and warm temperatures generally promote microbial proliferation, which can lead to increased biodeterioration of artifacts. Recent studies have highlighted the impact of climate change, showing that rising temperatures and shifts in humidity patterns are altering microbial colonization trends at heritage sites [16].

Material composition

The intrinsic properties of artifacts, including their organic or inorganic nature, porosity, and chemical composition, dictate their susceptibility to microbial colonization. Organic materials like wood and textiles are more prone to microbial attack, whereas the mineral composition of stones can influence which microbial species colonize their surfaces [17].

Mechanisms of Microbial Preservation

Microorganisms play a critical role in both the preservation and degradation of cultural heritage materials. Understanding the microbial mechanisms that contribute to artifact stabilization is essential for the development of effective conservation strategies. Certain microbial processes facilitate the protection of archaeological materials by forming mineral-binding biofilms, inhibiting biodeteriorative species, and chemically stabilizing artifacts [11].

A significant preservation mechanism is microbially induced calcite precipitation (MICP), which facilitates the formation of mineral-binding biofilms. This process is primarily mediated by Bacillus species, which hydrolyze urea, generating carbonate ions that react with environmental calcium ions to form calcium carbonate (calcite) [18]. The precipitated calcite crystals fill microscopic pores and cracks in

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stone artifacts, thereby reinforcing their structural integrity and reducing vulnerability to weathering and erosion. Studies have demonstrated that MICP effectively decreases the porosity of monumental stones, thereby limiting the infiltration of water and pollutants that contribute to deterioration [19].

Another crucial mechanism is microbial antagonism, wherein beneficial microbial communities outcompete harmful, biodeteriorative microorganisms through competitive exclusion. Protective microbes inhibit colonization by degradation-inducing species by depleting nutrients and producing antimicrobial compounds [20]. For example, certain bacterial strains secrete metabolites that suppress the growth of fungi known to degrade organic materials in archaeological structures. By establishing dominant microbial populations, these beneficial species help maintain artifact stability and minimize biodeterioration [21].

Microbially induced chemical stabilization is another preservation mechanism that plays a key role in artifact protection, particularly in metal artifacts. Bioleaching processes mediated by specialized microbial communities enable the removal of harmful metal ions responsible for corrosion. By sequestering reactive ions, these microbes prevent oxidation and mineral dissolution, thereby mitigating structural degradation. Furthermore, some bacteria can transform soluble metal ions into stable, insoluble forms, reducing their mobility and reactivity. This transformation minimizes the formation of corrosive compounds, ensuring the long-term stability of metallic heritage objects [22].

Distinguishing between beneficial and harmful microbial communities is a central challenge in conservation science. While some microorganisms actively contribute to preservation, others accelerate decay through acid production, enzymatic degradation, and biofilm formation. For instance, certain fungi generate organic acids that dissolve mineral components in artifacts, leading to irreversible damage. Thus, conservation efforts must prioritize strategies that sustain protective microbial communities while mitigating the impact of harmful species. This requires a thorough understanding of the microbial ecology of cultural heritage materials, as well as the environmental factors that influence microbial colonization and activity [23].

Analytical Techniques for Studying Archaeological Microbiomes

The study of archaeological microbiomes has advanced significantly with the integration of various analytical techniques that enable the characterization of microbial communities associated with artifacts and historical sites. These methodologies encompass microbial DNA sequencing, imaging modalities, stable isotope analysis, and non-destructive approaches, collectively enhancing our understanding of microbial roles in the preservation and degradation of cultural heritage [24].

Microbial DNA sequencing methods

Microbial DNA sequencing has become a cornerstone in microbiome research, facilitating the identification and characterization of microbial diversity within archaeological contexts. Two primary approaches are employed:

16S rRNA gene sequencing

This targeted method amplifies and sequences the 16S ribosomal RNA gene, a conserved region presents in all bacteria and archaea, allowing for taxonomic identification and assessment of microbial community composition [25].

Metagenomics

This comprehensive approach involves the direct sequencing of total DNA extracted from a sample, enabling the identification of all microbial genes present. Metagenomics provides insights into both the taxonomic diversity and functional potential of microbial communities, revealing metabolic pathways and ecological roles [26].

Imaging techniques

Advanced imaging techniques are crucial for visualizing microbial interactions with artifacts at microstructural levels:

Electron Microscopy

Scanning Electron Microscopy (SEM) and Transmission Electron Microscopy (TEM) provide high-resolution images of microbial cells and biofilms on artifact surfaces. These techniques enable the observation of biofilm architecture, microbial colonization patterns, and interactions with substrate materials, offering insights into biodeterioration processes [27].

Raman spectroscopy

This non-destructive technique utilizes inelastic scattering of monochromatic light to identify molecular compositions. In archaeological microbiome studies, Raman spectroscopy detects microbial-induced mineralogical changes, such as biomineralization processes, aiding in understanding microbial contributions to artifact preservation or degradation [28].

Stable isotope analysis

Stable isotope analysis involves measuring the ratios of stable isotopes (e.g., carbon, nitrogen) within materials to infer biogeochemical processes. In the context of archaeological microbiomes, this technique can:

Identify microbial metabolic activity

Variations in isotope ratios can indicate specific microbial metabolic processes, such as sulfate reduction or methanogenesis, which may influence artifact preservation.

Trace environmental conditions

Isotopic signatures can reflect past environmental conditions, offering insights into the depositional environment and potential microbial interactions over time [28].

Non-destructive microbiome analysis

Preserving the integrity of archaeological artifacts while studying their associated microbiomes necessitates non-destructive analytical methods:

Surface swabbing

Gentle swabbing collects microbial samples from artifact surfaces without causing damage, allowing for subsequent DNA extraction and analysis.

In situ spectroscopy

Techniques like Fourier-transform infrared spectroscopy (FTIR) and Raman spectroscopy enable the analysis of

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microbial communities and their metabolic products directly on artifacts, minimizing the need for sample removal [29].

Case Study of Ajanta Caves

The Ajanta Caves, located in Maharashtra, India, are a series of 30 rock-cut Buddhist monuments dating from the 2nd century BCE to the 5th century CE. Renowned for their intricate sculptures and murals, these caves have been designated a UNESCO World Heritage Site. However, they face significant preservation challenges, notably due to microbial degradation.

Challenges of microbial degradation

The deterioration of the Ajanta murals is exacerbated by the proliferation of microbial communities, including fungi and bacteria. The murals were executed on substrates comprising mud plaster mixed with organic materials such as paddy husks and vegetable fibers, overlaid with lime, kaolin, or gypsum. This organic-rich base provides an ideal environment for microbial colonization. Microorganisms, particularly fungi, metabolize these organic components, leading to structural weakening and visible damage to the paintings. Environmental factors, such as water seepage, further exacerbate microbial growth, compromising the integrity of the murals [30].

Identification of microbial communities

Studies have identified various microbial taxa present on the cave surfaces. Fungal species such as Aspergillus, Penicillium, and Cladosporium have been detected, along with bacterial genera including Bacillus and Pseudomonas. These microorganisms contribute to biodeterioration through enzymatic activities that degrade organic binders and pigments [Figures 1 and 2]. Advanced molecular techniques, including DNA sequencing, have facilitated the detailed characterization of these microbial communities, enhancing our understanding of their roles in the degradation processes [31].

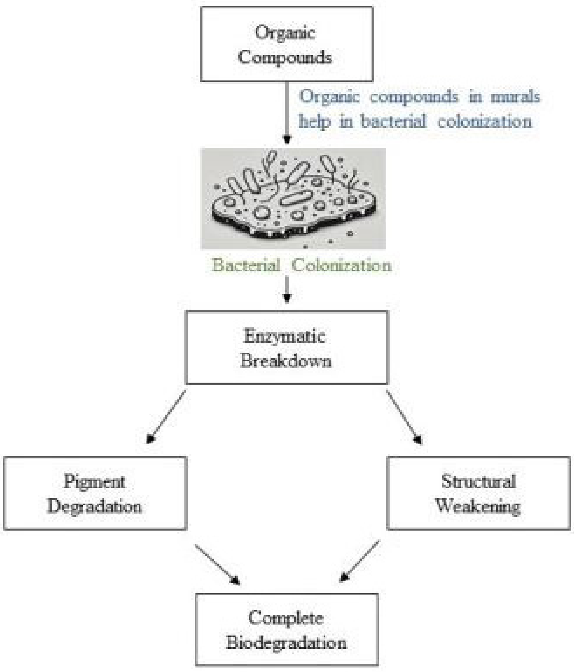

Figure 1. Bacterial Degradation of Organic Compounds in Murals

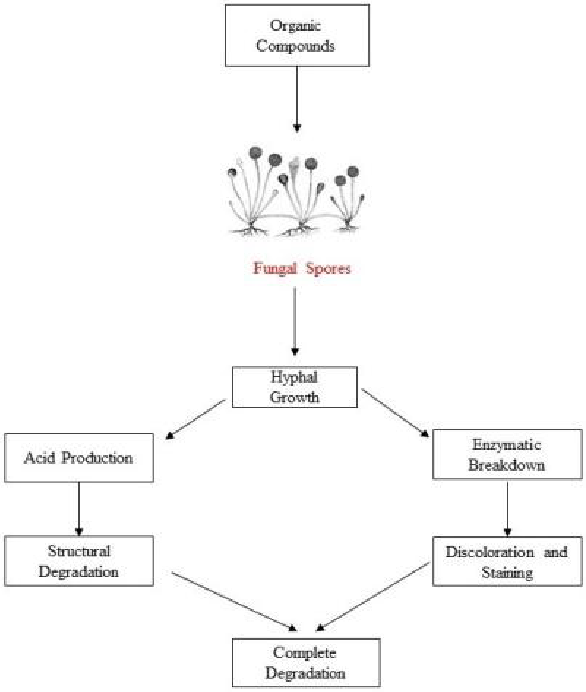

Figure 2. Fungal degradation of organic compounds in murals

Role of protective microbial layers

Recent research has explored the potential of harnessing beneficial microbial species to form protective layers on stone surfaces. Certain bacteria, such as those from the Bacillus genus, can induce the precipitation of calcium carbonate, leading to the formation of biogenic mineral layers that protect underlying surfaces. This biocalcification process not only consolidates the stone material but also inhibits the colonization and spread of harmful fungi by reducing available niches and altering surface properties [32].

Conservation strategies

To mitigate microbial-induced deterioration, conservation strategies have been developed focusing on microbiome regulation

Promotion of protective species

Microbiological techniques aim to introduce or encourage the growth of beneficial bacteria capable of biocalcification. By fostering these protective microbial layers, the structural integrity of the murals can be enhanced, and susceptibility to harmful microbial colonization reduced [33].

Microbiome regulation

Targeted removal of aggressive fungal species is achieved through the application of specific biocides or by altering environmental conditions to favour protective microbial communities. This approach requires a delicate balance to ensure that interventions do not adversely affect the murals or the surrounding ecosystem [34].

Challenges and Future Perspectives

Managing microbiomes at archaeological sites is complex, as microbial communities can be both beneficial and harmful.

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Accurately identifying microbial species is a major challenge, as environmental contamination can obscure native microbial populations. Studies using 16S rRNA sequencing face amplification biases, complicating taxonomic profiling and leading to inaccurate microbiome reconstructions. Biofilms present a conservation paradox. Some biofilms act as protective layers against environmental stressors, while others degrade surfaces through organic acid and enzymatic activity. The complexity of microbial interactions, including those between bacteria, fungi, and archaea, makes conservation efforts challenging. Effective strategies must balance biofilm removal with the preservation of protective microbial layers [35].

Genetic engineering, including CRISPR-Cas9, is being explored to enhance beneficial microbial traits and suppress harmful ones. However, its application to conservation is in the early stages and requires further technological advancements. Another approach involves artificially seeding microbiomes tailored for artifact protection. By designing synthetic microbial communities, harmful organisms can be outcompeted, leading to stable, protective biofilms. 3D scanning and modelling of microbiome-covered sites provide non-invasive ways to document microbial colonization over time. This digital approach enables real-time monitoring of microbial dynamics and aids in the development of targeted conservation strategies without direct sampling [36].

Conclusions

Microbiomes exhibit a dualistic role in cultural heritage conservation, acting as agents of both preservation and degradation. Certain microbial communities contribute to biodeterioration through processes like biofilm formation and acid production, leading to material decay. Conversely, specific microbes have been identified that can induce protective effects, such as the precipitation of calcium carbonate, which reinforces structural integrity.

Addressing these complex interactions necessitates an interdisciplinary approach, integrating microbiology, materials science, and archaeology. Such collaboration enables a comprehensive understanding of microbial dynamics and their impact on artifacts, facilitating the development of effective conservation strategies. For instance, insights into microbial colonization patterns can inform preventive measures, while materials science contributes to the creation of compatible conservation materials.

Embracing sustainable conservation strategies is imperative for the long-term preservation of cultural heritage. This includes leveraging beneficial microbial properties, such as employing bio mineralization processes to stabilize deteriorated structures. Additionally, incorporating eco-friendly materials and methods aligns conservation practices with environmental sustainability goals. By fostering interdisciplinary research and adopting sustainable methodologies, we can enhance the preservation of cultural artifacts, ensuring their endurance for future generations.

Disclosure statement

No potential conflict of interest was reported by the authors.

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