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Review

Microbial biodeterioration of cultural heritage and identification of the active agents over the last two decades

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ABSTRACT

Cultural heritage includes everything that mankind has created in the past and has impacted the development of culture. These objects can be subject to biodeterioration, including the activity of microorganisms, which can lead to the incalculable loss of records of our history. Therefore, it is essential to identify the microorganisms present on the surface of historical objects, monitor their metabolic activity, and based on this knowledge, find a possible way to protect the cultural heritage. This paper focuses on the most endangered cultural heritage objects (wooden objects, written documents, audio-visual materials, textiles, stone objects, paintings, and stained-glass windows), describes the materials that these objects are made of and the reasons for their biodeterioration. Furthermore, we provide an overview of all microbial identification methods used in the field of cultural heritage since 2005, when the first next-generation sequencing technique originated.

Introduction and research aim

Cultural heritage is commonly perceived as a connection between the past and the present. Since it is unique and irreplaceable, the effort to preserve it for future generations is unquestionably relevant [1]. Cultural heritage covers a variety of things, from stone and wooden objects to certain works of art, such as paintings, photographs, cinematographic films, books, or parchments [2]. In addition to their intrinsic degradation factors, these objects are still exposed to abiotic and biotic factors, which result in the degradation of their materials [3]. It is important to determine all these factors influencing culture heritage biodeterioration.

In the 1980s, it was agreed that microbial activity might be the main reason for the deterioration of historical objects [4,5]. Microorganisms have versatile metabolic abilities – they can damage both organic-based materials (paper, leather, parchment, textiles, or wood) and inorganic-based materials (glass or stone) [4,6]. Several review articles dedicated to the biodeterioration of selected cultural objects have already been published. For example, Cappitelli and Sorlini [7] described the biodeterioration of documentary heritage materials, Griffin, et al. [8] and Warscheid and Braams [9] the biodeterioration of stone, Blanchette [10] and Clausen [11] the biodeterioration of wood, and Szostak-Kotowa [12] the biodeterioration of textiles.

To prevent biodeterioration, and consequently safeguard cultural heritage objects, it is necessary to identify the microorganisms present, both bacteria and fungi. Bacteria are a very diverse group of microorganisms that are involved in the production of colour and pigment, and their metabolic activities thus negatively affect cultural objects. Fungi, on the other hand, are more resilient than bacteria. For instance, they are more resistant to drying out, and they benefit from spore diffusion as a transport mechanism. Fungi also produce a wide range of organic acids and provide mineral nutrients to other microorganisms, especially phototrophs [13]. An overview of available methods for the identification of microorganisms from cultural heritage objects is already provided, for instance, in the articles by Otlewska, et al. [14], Perito and Cavalieri [15], Sanmartin, et al. [16], or Gutarowska [2]. However, there is no comprehensive overview of cultural heritage objects, including their biodegradation processes and the methods that have been successfully used for the identification of biodeterioration agents.

This review aims to provide a summary of the threatened cultural objects that are subject to biodeterioration. High emphasis is

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placed on the damage that these microorganisms can cause. It also provides an overview of all studies that have analysed the biodiversity of cultural heritage objects. Despite the ever-increasing popularity of culture-independent methods, such as sequencing and, above all, next-generation sequencing (NGS), we have decided to show that culture-dependant methods are also still on track. Thus, studies using both culture-dependant and culture-independent methods are presented, dating back to the inception of the first NGS method, pyrosequencing.

An overview of cultural heritage objects

Wooden objects

Wood is a traditional building material [17]. In the past, wood was used to produce shelters, furniture, or ships, and its destruction leads to the loss of cultural resources [10]. Archaeological wood can also be found in ancient burial grounds, such as in Egypt, where wood carries important information about ancient cultures. Due to biodeterioration, wood in such cemeteries is usually in an advanced state of decay.

For wood preservation, knowledge of its composition is essential [18]. It consists of cellulose (40–50%), hemicellulose (15–25%), and lignin (15–25%). According to hemicellulose and lignin content, a distinction is made between hardwoods and softwoods. Unlike softwoods, hardwoods contain more hemicellulose and less lignin [19].

The decomposition of wood can be caused by both bacteria and fungi. Bacteria can be divided into three groups based on the damage they can cause: erosion, tunnelling and cavitation [10]. The first one, erosion bacteria (EB), include bacterial species from the groups Flavobacteria and Cytophaga [20]. They are able to tolerate a wide range of temperatures and humidity levels, and they occur mainly in environments with low oxygen concentrations. For this reason, degradation by EB is often associated with buried and waterlogged archaeological wood [19]. EB on the surface of the wood can penetrate into the cell lumen via pits. From there, the bacteria attack the secondary cell wall of the wood, which is rich in cellulose, and convert it into amorphous material [20]. Moreover, erosion troughs are formed on the exposed areas of the cell wall. This phenomenon can be observed by transmission electron microscopy (TEM) [19]. However, the lignin-rich lamellae remain intact. This inability to break down lignin is the reason why wood still retains its form and integrity in a humid environment [20]. Second, tunnelling bacteria (TB) cause tunnels within the secondary cell wall. An example of a tunnelling bacterium is *Clostridium xylanolyticum*, which was the first isolated bacterium of this kind [21]. Unlike EB, they require a higher amount of oxygen and can only degrade lignin to a limited extent. In addition, they are able to degrade the middle lamella of plant cells [10,22,23]. Their attack is usually observed with soft rot fungi or EB attack [19]. Third, cavitation bacteria (CB) create very small cavities within the secondary cell wall, which enlarge over time in diamond shapes. As the decay becomes worse, the neighbouring cavities merge and form irregular cavities [10,24]. Their utilisation of lignin was not observed [10]. However, cavitation bacteria are scarcely covered in the literature, and further research needs to be done.

The fungal biodegradation of wood is also significant. Fungi penetrate the wood with hyphae and can use the wood as a source of nutrition. Some fungi live only on cellulose, others also on lignin [11]. amongst the primary degrading fungi are those that cause white, brown, and soft rot [25,26]. These are mostly mushrooms rather than microscopic fungi, which are not as important from the microbial point of view. That is why we only describe the rots briefly. First, brown rot is the most important wood-degrading rot in buildings in Europe and North America [25]. During the process of brown rotting, the wood acquires a browner colour, and only the cellulose is being removed, which causes the wood to collapse and pulverise. Brown rot fungi usually colonise softwood [11]. Second, white rot, which mainly attacks hardwoods, is less common [25]. This rot usually decomposes cellulose and lignin, so the wood can lose colour and look whiter. However, brown- and white-rot fungi can sporadically attack both types of wood. The last type, soft rot, usually affects only the surface of the wood and is therefore the most dangerous for thin pieces of wood. When wet, it can soften, but below the rotted area, the wood can still be healthy [11].

Written documents

Paper and parchment are amongst the most critical treasuries of human recorded history. Old books, manuscripts, or documents, are all made of paper, parchment, or both [27]. However, these materials are a suitable source of energy, carbon, and nitrogen for many microorganisms. This often results in microbial damage that can deform them and hence make them unreadable [28]. Preserving these objects is therefore becoming a real challenge [29].

Paper. The invention of paper dates to the 1st century A.D. in China. In the 12th century, paper appeared in Europe and gradually became the most common writing material around. Paper is made of vegetable fibres with cellulose as their main compound. The paper is further treated with materials such as starch, gelatine, or synthetic polymers to prevent the spread of ink. In addition, clays or chalks are used to fill its pores [7].

A critical factor that plays a significant role in paper damage is the presence of dust, which contains fungal spores that settle on the paper surface. Under suitable temperature and humidity conditions, fungi can multiply on the surface and cause significant damage [29]. Fungi play a major role in the biodeterioration of paper. Typical species that colonize this material are slow-growing Ascomycetes and xerophilic species, i.e., those that grow even with low water activity. These include the genera *Aspergillus, Paecilomyces, Chrysosporium, Penicillium* and *Cladosporium* [30]. Other genera can appear after a sudden penetration of water into the archive, for example during floods or due to pipeline damage. Some microscopic sponges that require higher water activity can then easily grow and degrade materials. These include, for example, *Stachybotrys* spp., *Chaetomium* spp. or *Epicoccum* spp. [31].

The activity of microorganisms can cause brownish or reddish spots to form on the paper. The formation of such spots is referred to as foxing [7], and the main originators are xerophilic fungi of the genera *Aspergillus, Cladosporium, Penicillium* and *Eurotium*. These spots are likely to result from: i) the secretion of phenolic pigments by the mycelium; ii) The Maillard reaction (cellulose degradation products react with mycelial amino acids); iii) the autooxidation of fungal lipids [32]. Besides the aesthetic changes, structural damage (decomposition of paper components) can also occur [29]. Cellulolytic enzymes (exoglucanase, endoglucanase, and β-glucosidase) can degrade cellulose structure, which leads to depolymerisation and causes paper fragility [29,33].

Parchment. Parchment began to be used mainly around the 3rd century A.D. when it replaced Egyptian papyrus. Its advantages include firmness and better durability compared to papyrus, thanks to its main component – collagen. Moreover, collagen was broadly available as a main component of animal skin [7].

The usage of parchment was widespread, especially in the Middle Ages. Despite it being considered essential for cultural heritage, studies on the microbial contamination of parchment are still limited [34]. However, the causes of biodegradation are already known. The primary microbial contaminant found on parchments

is bacteria. The reason is that parchment has a higher pH level, which is more suitable for bacteria than targeted fungi [28]. Nevertheless, parchment is suitable for some proteolytic fungal genera: *Cheatomium, Gymnoascus, Aspergillus, Aureobasidium*, or *Trichoderma*. However, the main role is played by a bacterial hydrolytic enzyme called collagenase, which involves oxidative damage to amino acid chains and hydrolytic cleavage of the peptide structure. Collagenase-producing genera, such as *Bacillus, Staphylococcus* or *Pseudomonas*, have already been isolated from parchment. In addition, microorganisms can produce pigments and organic acids, which may result in discoloration. For instance, the formation of purple spots is typical for parchment. These spots are often associated with alkaliphilic bacteria [30]. Lastly, the content of oil and waxes can be utilised by microorganisms as a carbon source [35].

Textiles

Materials that are made of fibres and threads are called textiles. Examples are fabrics, furs, or carpets. Based on their origin, we can divide the fibres into natural and chemical [36]. Historical textiles are usually made of natural organic fibres, such as plant fibres: cotton, linen, hemp, and jute, or animal fibres: wool, silk, or leather. These are easily degraded by microorganisms [12,37]. In contrast, chemical fibres are made from modified natural or synthetic substances and are classified as artificial (viscose) or synthetic (polyester, acryl, PVC fibres), and are generally more resistant to biodegradation [36]. In synthetic fabrics, finishing agents (adhesives, dyes) are subject to biological damage more than the fibre itself [12].

Textiles are regarded as a nutrient-rich environment, so both bacteria and fungi can thrive on them [5]. Both bacteria and fungi have already been isolated from historical textiles, but mainly fungi are considered to be the main degrading agents [37]. The reason for this is that the fungal production of cellulolytic and proteolytic enzymes (same microbial enzymes as for paper and parchment, respectively) is one of the highest risk factors for the deterioration of historical textiles [38]. Other risk factors include the production of acids and the excretion of pigments. The loss of strength, extensibility, changes in colour, appearance, and pH are some of the most common impacts [38,39]. In addition, fungi are difficult to remove from textiles, because their hyphae can grow not only on the surface, but also inside the fibres [37].

The degradation of historical textiles depends on many conditions, such as the wear rate, the type, temperature, and humidity conditions [36], since the textile can absorb and retain moisture from the environment [38]. The degree of damage increases considerably when in contact with soil and water, especially in warm and humid climates [36]. Another condition that may be responsible for deterioration is ultraviolet radiation, which causes oxidation of the polymers that form natural fibres and allows the penetration of microbial enzymes [37].

Cotton, linen, jute, and hemp are plant-derived fabrics. Therefore, they are subject to cleavage by lignocellulolytic enzymes. The main role is played by cellulases, which cause the depolymerisation of cellulose, and consequently a reduction in the strength of the material. Another component of the plant cell wall, hemicellulose, is also easily degraded by cellulolytic organisms. Resistance to degradation is supported by the content of lignin. For example, jute and hemp, which have a higher lignin content, are degraded more slowly than cotton, which lacks lignin [5]. Examples of cellulolytic bacterial genera are *Arthrobacter, Microbispora, Sporocytophaga, Cellulomonas, Bacillus, Cellvibrio, Clostridium, Cytophanga, Pseudomonas, Nocardia*, or *Streptomyces*, while examples of cellulolytic fungal genera are *Aspergillus, Chaetomium, Mnemoniella, Stachybotrys, Verticillium, Penicillium, Mucor, Trichoderma, Myrothecium, Rhizopus, Alternaria, Fusarium, Aureobasidium*, or *Cladosporium* [40].

Animal fabrics, such as wool, silk and leather, are more resistant to degradation [5]. Their main components are proteins: keratin in wool and leather, fibroin and sericin in silk [40,41]. For this reason, animal fabrics are primarily sensitive to proteases. Keratin is composed of antiparallel peptide chains, which are additionally crosslinked by disulfide bridges. First, the disulfide bridges are reduced, making the peptide chain suitable for protease attack. Degradation of the peptide can lead to the formation of ammonia, due to deamination of acids [5]. Keratinolytic bacterial genera include *Alcaligenes, Bacillus, Proteus, Pseudomonas*, or *Streptomyces*. Keratin-degrading micromycetes include the genera *Acremonium, Alternaria, Dematium, Stachybotrys, Fusarium, Rhizopus, Aspergillus, Penicillium, Microsporium, Trichophyton, Trichoderma* and *Chaetomium* [40]. As was mentioned above, silk is composed of two main proteins: fibroin (consisting mainly of glycine, alanine, serine and tyrosine), which forms fibers, and sericin, which acts as an adhesive. A lower rate of degradation was demonstrated on sericin-free textiles. Therefore, it is reported that sericin is the main protein utilised by microorganisms as a nutrient. However, even fibroin can be utilised by some microorganisms, such as the bacterium *Pseudomonas cepacia* as well as one fungal strain, *Aspergillus niger* [12].

Audio-visual materials

Audio-visual materials are used to store information that can be retrieved by hearing, seeing, or both. They can be divided into three groups: i) audio materials – vinyl records, tapes; ii) visual materials – photographs or silent movies; iii) both audio and visual – cinematographic films [42]. Historical photographs and cinematographic films from museums, archives, but also private collections are also part of cultural heritage [43]. These objects have emerged mainly over the last two centuries. Several techniques for producing these materials have been applied during that period, which allows their classification into specific decades [42].

Photographs and cinematographic films consist mostly of two main layers: the carrier and the photosensitive emulsion [44]. This photographic emulsion usually consists of an image-forming material (silver particles for black and white images) and a binder [45]. Gelatine, albumen, and collodion have been most frequently used as binders throughout history [46].

As with other cultural objects, an increase in humidity is a critical factor in the initiation of the biodegradation of audio-visual materials. Damage can be caused by enzymes, such as proteinases and cellulases, which can destroy all material layers [43]. Also, microbial colonies can appear as colour spots (black, brown, yellow, white or other colours) [47]. This phenomenon of staining is called foxing (this term is also used with paper, as mentioned above) and is explained in more detail in a review by Tepla, et al. [42]. The appearance of stains can lead to a loss of image sharpness. In addition, fungi can degrade photos and films through hyphae that penetrate the binder and carrier [43].

Gelatine, a common binder, is a highly biodegradable biopolymer produced by collagen denaturation, and was used primarily in the 19th century to create positives and negatives [46,48]. The main disadvantage of gelatine is that it can be easily colonised by microorganisms with proteolytic properties, such as *Bacillus, Clostridium, Micrococcus, Enterococcus, Aeromonas, Serratia, Burkholderia, Yersinia, Salmonella, Pseudomonas, Staphylococcus*, and *Streptococcus*, which are amongst the most frequently isolated bacteria genera from audio-visual materials [5,42,43]. Fungal genera with proteolytic properties, such as *Aspergillus, Penicillium, Trichoderma, Cladosporium, Mucor, Alternaria, Phoma*, and *Cryptococcus*, have also been isolated from audio-visual materials

[5]. This colonisation regularly results in gelatine liquefaction, and consequently in the decay of audio-visual materials [43]. Albumen was the most common binder for photographs on paper during the 19th century [46,49]. Albumen is a biodegradable protein obtained from egg whites, and is easily utilised by microorganisms with alkaline serine proteases, such as the bacterial genera *Bacillus, Arthrobacter, Streptomyces*, and *Flavobacterium*, and fungal genera *Conidiobolus, Aspergillus* and *Neurospora* [50,51]. Collodion, which contains cellulose nitrate, was largely popular between 1890 and 1920 [7,52]. It allowed for a wide range of colours – from reddish-brown to deep black. Nonetheless, collodion prints were rippled in the bath during photo development, and they were susceptible to chemical impurities. This reason led to its loss of popularity after a few years [52]. Moreover, collodion can be affected by cellulolytic fungal species, such as from the genera *Aspergillus, Penicillium*, or several others already mentioned in chapter 2.3 on textiles [53]. However, it is mainly oxidants that are responsible for staining and yellowing [54].

Since the invention of cinematographic film, several types of carriers have been used, such as cellulose nitrate, cellulose diacetate (later cellulose triacetate), and polyethene terephthalate. Cellulose nitrate, used mainly in the first half of the 20th century, is highly flammable. For this reason, cellulose diacetate started to be used as an alternative in the second half of the 20th century. While flammability was not the issue, the main problem was sensitivity to so-called vinegar syndrome, i.e., the deacetylation of acetate by esterases, forming acetic acid [5,55]. Many studies were focused on reducing the damage caused by vinegar syndrome [45]. The degradation of acetate has been demonstrated in the fungal genera *Aspergillus, Penicillium, Fusarium* and *Trichoderma*, as well as the bacterial genera *Pseudomonas* and *Neisseria* [5]. The last of them, polyethene terephthalate, has been used since 1990 and is characterised by its chemical stability [55]. However, contamination by microorganisms remains an unresolved problem for this material. There are ways in which microbial populations can disrupt the structure of the polymeric materials used today. In addition to pigment contamination, they can also penetrate the polymeric materials [45].

Stone objects

Whether we are talking about prehistoric caves or modern buildings, stone has always served as a protective material [56]. From a microbiological perspective, stone represents an extreme environment low in nutrients and exposed to constant weather changes when outdoors [41]. Nevertheless, various microorganisms from phototrophic to heterotrophic have been identified on the surface of stone cultural objects in all climatic regions [13,41]. The most suitable climate for the colonisation by microorganisms is the tropical climate, which is abundant in moisture and sunlight, both critical for microbial growth [13]. Stone biodeterioration can occur due to:

i) colonisation by phototrophic microorganisms that form biofilms. These are mainly algae or cyanobacteria (for example, genera *Fischerella, Eucapsis, Leptolyngbya*) [5], which require light and moisture for their growth. These organisms can be either on the surface or penetrate through stones pores and cause physical and chemical damage [57,58]. They participate in disintegrating the crystalline structure of some rocks, such as sandstone, granite, limestone, or even bricks. Phototrophic microorganisms can also secrete carbohydrates and growth factors which facilitate complex biofilm formation [57].
ii) microbial pigment production. Algae and cyanobacteria are responsible for discoloration (green, black, etc.). During photosynthesis, both algae and cyanobacteria form photosynthetic pigments that cause changes in surface colour. Black fungi also cause discoloration of the stone. However, in this instance it is not photosynthetic pigments, but melanin produced by fungi which turns the surface of the stone black-brown [59]. Stone objects can also be colonized by halophilic archaea (*Halobacterium, Halococcus*), which grow in a salty environment and can produce a pink pigment [5].
iii) the presence of microbial acids. Some microorganisms can excrete organic acids, which chelate metal cations (Al, Ca, Fe, Mg, Mn, Si) from the stone and form stable complexes. Some microorganisms (bacteria of the genus *Bacillus, Leptospirillum*, or yeast-like fungi of the genus *Aureobasidium*) can remove cations of manganese, or iron by oxidation [60]. Furthermore, even inorganic sulfuric acid can be produced on the surface of the stones. That is an aftereffect of the presence of sulphur-oxidising bacteria (*Thiobacillus* spp.) [60,61]. The acid can then react with the stone components, resulting in a sulfate-based crust [60]. Next, nitrous and nitric acids can be excreted by nitrifying bacteria, such as *Nitrosomonas* spp., *Nitrobacter* spp., *Nitrosovibrio* spp., and *Nitrosospira* spp. [62,63]. Nitrifying bacteria are chemolithoautotrophic microorganisms, and they are able to oxidise ammonium to nitride, and ultimately to nitrate [62]. Via the action of nitrides, the stone is dissolved and nitrate acids are formed [61,63].
iv) the penetration of fungal hyphae deep into the stone [60]. The penetration is up to several centimetres to find nutrients. This process frequently leads to weathering of the material. Moreover, the cell walls of fungi contain melanin and humic substances, which can colour the surface of the stone to shades of brown or black. The most important genera of micromycetes that degrade stone include *Cladosporium, Penicillium* or *Trichoderma* [64].

Paintings

Traditionally, paintings have been used since ancient times and provide us with a great deal of useful information. Thus, they are understood as valuable works of art [65]. For instance, the unique cave paintings in Lascaux discovered in 1940 bring us information from the Late Stone Age dating to 15 000 to 13 000 BC. There are up to 600 paintings in the cave, which, with a few exceptions, represent the various animals living at that time [66].

Paintings contain a wide range of organic and inorganic components [67]. Many of them are biodegradable and can be used as substrates for a wide range of microbial species [68,69]. Of these biodegradable substances, additives such as adhesives, emulsifiers, or thickeners were extensively used to make it easier to use or apply paint in layers [66,70]. Moreover the effect of other organic components added during art restoration, and the presence of pollutants that accumulate on the surface, can also cause damage [66,71].

Paintings can be loosely classified into two categories: mural paintings, where the paint is applied directly to a wall, and easel paintings, where the artist uses an easel to apply paint to various foundations (paper, canvas, parchment, silk, or wool). If we compare both types of paintings from the microbial point of view, easel paintings seem to be more suitable for microbial colonisation. The main reason is that the carrier material used for easel paintings is easily decomposable for microorganisms. In addition, easel paintings also contain other organic molecules such as sugars, proteins, oils, waxes, egg yolks, bile, or even urine [66,67]. This wide range of substances allows the growth of many bacteria and fungi on the surface of paintings [72]. In contrast, walls are generally composed of inorganic materials, which are less suitable for microbial growth, and therefore the microbiota differs considerably from that of easel

paintings [66,72]. It was found that despite the unfavourable conditions, a wide range of fungal genera can appear on murals. These include *Aspergillus, Penicillium, Cladosporium, Alternaria, Curvalaria, Dreschlera, Chaetomium, Fusarium, Trichoderma, Gliomastk*, and *Aureobasidium* [65]. This contamination occurs mainly with the secco technique, where, unlike the fresco technique, the pigments are dispersed in a binding medium (e.g. eggs or organic substances) before applying to a dry plaster [73].

Most of the fungal genera associated with the biodegradation of canvas paintings can produce cellulolytic enzymes to dissolve cellulose fibres [30]. These genera were also mentioned in chapter 2.3 on textiles. Frequent bacterial contaminants with biodegradation ability include the genera *Pseudomonas, Bacillus* or *Staphylococcus* [74,75]. Previous bacterial colonisation can facilitate colonisation by fungi, commonly by the genera *Aspergillus, Penicillium* or *Cladosporium* [69,74]. Some of the microorganisms mentioned above also have the ability to separate the colour layer from the substrate. In addition, microbial populations can form both organic and inorganic acids as metabolic products, resulting in the material loss of the carrier. Finally, biodeterioration occurs due to the activities of various enzymes, including lipases, esterases, endo-N-acetylglucosaminidases, and proteases [68].

Stained window glass

Stained-glass windows can be found in cathedrals and churches throughout Europe [76,77]. The stability of a glass depends on its chemical composition, the existence of the organic layer and the climatic conditions [78]. Stained glass is composed of several components: network formers (in the Middle Ages mainly silica and phosphorus), stabilisers, modifiers, and colouring elements, such as copper, cobalt or manganese [79].

The biodeterioration of stained window glass occurs in various ways due to the growth and/or metabolic activities of micromycetes, bacteria and lichens [79], which can accelerate physical-chemical processes leading to glass breakdown [77]. These processes are induced by cell growth, which is influenced by several factors, such as relative humidity, temperature, carbon concentration, glass moisture, or the chemical stability of the glass [80,81].

However, the colonization of glass by microorganisms can lead to several types of damage [80]. First, glass cracks can be expanded due to the growth of fibrous fungi [78]. Second, glass transparency can be disrupted by pigment-forming microorganisms or due to the oxidation of trace metals [76,78]. Third, damage can be caused by the production of organic and inorganic acids, which usually lead to changes in pH, to the chelation of glass components and thus to the destruction of the glass [78,79]. In fact, it was shown that the main contaminants of glass are mainly microscopic fungi that produce acids [80]. Fourth, a process called leaching may occur. During this process, the mass of the glass as well as the amount of network modifiers decrease. This results in a gel surface, and the leached elements can react with atmospheric compounds to form complex salts. The most soluble salts are removed by rain and moisture, while the others form crusts and patinae on the surface of the glass [81].

The most harmful microorganisms are fungi, due to the resistance of spores to drying out, their ability to adhere to a hydrophobic substrate, and their ability to metabolise a wide range of carbon sources. It has also been shown that chemical and morphological changes occur upon the inoculation of fungi on glass samples in a short period of time [77]. Species commonly identified on glass include *Aspergillus, Cladosporium, Trichoderma, Penicillium, Chaeromium, Aureobasidium, Eurotium, Phoma, Scopulariopsis*, and *Rhizopus* [82].

Identification methods

The main aim of identifying microorganisms on cultural heritage objects is to prevent their degradation. It is therefore fundamental to choose methods that will provide us with a comprehensive overview of the microbial populations in a given environment [16]. Despite the fact that it has been 16 years since the first next-generation sequencing (NGS) method was established, cultivation-dependant methods still predominate. Besides the culture-dependant methods, various other identification techniques have also been used, including Sanger sequencing, next-generation sequencing, and the third-generation sequencing method MinION, to name a few. Table 1 shows all available studies focused on microbial identification on cultural heritage objects since 2005, when pyrosequencing, the first NGS technique, was introduced.

Sampling

The first step in all microbiological analyses is the collection of samples. For sampling cultural heritage objects, it is necessary to select a sampling method that is friendly to the objects. Therefore, non-invasive or micro-invasive techniques are preferred. Unfortunately, with these techniques there can be the problem of a lack of material obtained for further analysis. Several different sampling approaches appear in the studies listed in Table 1.

When sampling for subsequent culture-dependant methods, swabs were chosen in most cases. It was only for stone objects that the use of micro-invasive techniques predominated, where the material was scraped with a scalpel, chisel or toothpicks. Micro-invasive techniques were also predominant when culture-independent methods were used. More specifically, for Sanger sequencing, DNA was most often isolated directly from materials that had been obtained either by scraping with a sterile scalpel, cutting out a section, or collecting sections that had already broken off and could not be incorporated back into the cultural object. In rare cases adhesive tape was used, a microinvasive technique that is gentle on the material being sampled while still collecting sufficient biological material, or a nitrocellulose membrane. The approach to sampling for analysis in studies using NGS is no longer very different from sampling for Sanger sequencing. For pyrosequencing, in the study by Migliore, et al. [98], small pieces of parchment already detached that could not be relocated during restoration were taken directly for analysis. For sampling textiles in Brzozowska, et al. [122], a non-invasive method using sterile and dry medical cotton buds was used. Cutler, et al. [133] used sterile adhesive tape for collecting samples. Vasanthakumar, et al. [196] used sterile swabs moistened in sterile de-ionised water or in sterile water with an added surfactant, Tween 80. In the final one, Rosado, et al. [193] used a micro-invasive method combining sterile swabs and scalpels. Sample collection for DNA isolation and subsequent sequencing using Illumina MiSeq was in most cases performed by scraping with a scalpel. Other techniques used were vacuuming on the surface, using swabs or adhesive tape. In some cases, only pieces of material were collected, from which DNA was subsequently isolated [43,100]. For Illumina HiSeq, a scalpel was used or material that had already fallen off was collected, and in both studies using Ion Torrent sequencing, scalpels were also used for sample collection.

For MinION, a different collection approach was used in each study. In the study by Grottoli, et al. [137], the authors used a microinvasive technique – adhesive tape. In the studies by Pinar, et al. [215,109], a non-invasive sampling technique was used. Specifically, Pinar, et al. [215] sampled using dry cotton swabs (3–5 swabs for one painting each time) while Pinar, et al. [109] used a micro-

Table 1
Overview of microbial biodiversity studies on selected cultural heritage objects (2005–2021) sorted based on the approach used.

Cultural heritage object		Culture-dependant methods[a]	Culture-independent methods[b]				
			Sanger	NGS			MinION
				Pyrosequencing	Illumina Solexa	Ion Torrent	
					HiSeq2500 MiSeq		
Wooden objects		de Carvalho, et al. [83]	**Palla, et al. [84]**		**Liu, et al. [85], [89]** Antonelli, et al. [86]		
		Grbic, et al. [87]	**Pinar, et al. [88][c]**		Gutarowska, et al. [90]		
		Ilies, et al. [91]					
		Kozirog, et al. [92]					
		Liu, et al. [85], [89]					
		Palla, et al. [84]					
		Pangallo, et al. [93,94]					
		Pinar, et al. [88]					
		Stafura, et al. [95]					
Written documents	Parchment	de Carvalho, et al. [96]	Pinar, et al. [97][c]	Migliore, et al. [98]	Pinar, et al. [99] Migliore, et al. [100]		
		Krakova, et al. [34]	Troiano, et al. [101][c]		**Perini, et al. [102]**		
		Lech [103]			Teasdale, et al. [104]		
		Perini, et al. [102]					
		Pinzari [105]					
	Paper	Borrego, et al. [53,106,111]	**Di Carlo, et al. [107]**		**Krakova, et al. [108]**		Pinar, et al. [109]
		Di Carlo, et al. [107]	**Michaelsen, et al. [110][c], [112][c]**		Szulc, et al. [32]		
		Jacob, et al. [114]	**Montanari, et al. [113]**				
		Krakova, et al. [34]	**Okpalanozie, et al. [29][c]**				
		Krakova, et al. [108]	**Pasquarella, et al. [115]**				
		Mesquita, et al. [118]	Principi, et al. [116] [c]				
		Michaelsen, et al. [110], [112]	Rakotonirainy, et al. [117]				
		Micheluz, et al. [119]					
		Montanari, et al. [113]					
		Okpalanozie, et al. [29]					
		Pasquarella, et al. [115]					
		Valentín [120]					
		Zotti, et al. [121]					
Textiles		Borrego, et al. [106,53]		Brzozowska, et al. [122]			
		Kavkler, et al. [37]					
		Omar, et al. [38]					
		Pietrzak, et al. [40]					
Audio-visual materials	Photographs	Borrego, et al. [53,123,106]	Buckova, et al. [124]		Branysova, et al. [125]		
		Grbic, et al. [87]	**Puskarova, et al. [49][c]**		Szulc, et al. [43]		
		Kwiatkowska, et al. [127]	**Sclocchi, et al. [126][c]**				
		Puskarova, et al. [49]					
		Sclocchi, et al. [128]					
		Sclocchi, et al. [126]					
		Abrusci, et al. [45]					
	Cinematographic films						
		Bingley and Verran [55]					
		Rakotonirainy, et al. [129]					
		Vivar, et al. [130]					

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Table 1 (*continued*)

Cultural heritage object	Culture-dependant methods[a]	Culture-independent methods[b]					
		Sanger	NGS				MinION
			Pyrosequencing	Illumina Solexa		Ion Torrent	
				HiSeq2500	MiSeq		
Stone objects	Abdelhafez, et al. [131]	**Adetutu, et al. [132]**[c]	Cutler, et al. [133]	Ding, et al. [134]	Bai, et al. [135]	Adamiak, et al. [136]	**Grottoli, et al. [137]**
	Adetutu, et al. [132]	Cennamo, et al. [141][c]			Chimienti, et al. [138]	Pinar, et al. [139]	
	Andrei, et al. [140]	**Ettenauer, et al. [144]**[c], **[148]**[c]			Dias, et al. [142]		
	Bader, et al. [143]	Jroundi, et al. [151][c]			**Dias, et al. [145]**		
	Boniek, et al. [147]	Jurado, et al. [155]			Ding, et al. [146]		
	Cappitelli, et al. [150]	**Krakova, et al. [156]**			**Dyda, et al. [149]**		
	De Leo, et al. [153,154]	Lan, et al. [157]			Gaylarde, et al. [152]		
	Dias, et al. [145]	**Lepinay, et al. [159]**			Gutarowska, et al. [90]		
	Dyda, et al. [149]	McNamara, et al. [160]			Jroundi, et al. [158]		
	Ettenauer, et al. [144], [148]	Meng, et al. [161,163]			Li, et al. [61]		
	Gallego-Cartagena, et al. [165]	**Pangallo, et al. [166]**			**Li, et al. [162]**		
	Gaylarde, et al. [168]	**Pinar, et al. [169]** [c]			**Rosado, et al. [164]**		
	Grottoli, et al. [137]	Pinar, et al. [171][c]			**Schroer, et al. [167]**		
	Hu, et al. [174]	**Polo, et al. [175]**[c]			**Soares, et al. [170]**		
	Jroundi, et al. [177]	**Zammit, et al. [178]**			Torralba, et al. [172]		
	Krakova, et al. [156]				**Trovao, et al. [173], [176]**		
	Lepinay, et al. [159]				Zhang, et al. [179]		
	Li, et al. [162]						
	Li, et al. [180]						
	Mandal and Rath [181]						
	Nuhoglu, et al. [182]						
	Pangallo, et al. [166]						
	Petraretti, et al. [183]						
	Pinar, et al. [169]						
	Pinar, et al. [184]						
	Pinna, et al. [185]						
	Polo, et al. [175]						
	Rosado, et al. [186]						
	Rosado, et al. [164]						
	Rotolo, et al. [187]						
	Savkovic, et al. [188]						
	Schroer, et al. [167]						
	Soares, et al. [170]						
	Trovao, et al. [189]						
	Trovao, et al. [173], [176]						
	Urzi and De Leo [190]						
	Zammit, et al. [178]						

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Table 1 (*continued*)

Cultural heritage object		Culture-dependant methods[a]	Culture-independent methods[b]					
			Sanger	NGS				MinION
				Pyrosequencing	Illumina Solexa		Ion Torrent	
					HiSeq2500	MiSeq		
Paintings	Murals, painted sculptures, frescoes	Biswas, et al. [191]	Bastian, et al. [192]	**Rosado, et al. [193]**		Duan, et al. [194,197]		
		De Leo, et al. [153]	Cuezva, et al. [195]	**Vasanthakumar, et al. [196]**		Ogawa, et al. [200]		
		Di Carlo, et al. [107]	**Di Carlo, et al. [107]**					
		Dupont, et al. [198]	Giustetto, et al. [199]					
		Heyrman, et al. [201]	**Heyrman, et al. [201][c]**					
		Kiyuna, et al. [202]	Imperi, et al. [203][c]					
		Ma, et al. [204]	**Ma, et al. [204]**					
		Rosado, et al. [205,210]	Portillo, et al. [206][c],[208][c]					
		Rosado, et al. [193]	Portillo and Gonzalez [207]					
		Saiz-Jimenez, et al. [209]	**Saiz-Jimenez, et al. [209][c]**					
		Vasanthakumar, et al. [196]	Zimmermann, et al. [211]					
		Zammit, et al. [212]						
		Zucconi, et al. [213]						
	Canvas	de Carvalho, et al. [83]	**Lopez-Miras, et al. [68][c], [216][c]**			de Carvalho, et al. [214]		Pinar, et al. [215]
		Ilies, et al. [91]	**Okpalanozie, et al. [217][c]**			Torralba, et al. [172]		
		Kavkler, et al. [37]						
		Lopez-Miras, et al. [68], [216]						
		Okpalanozie, et al. [217]						
Stained window glass		Pinto, et al. [82]	Carmona, et al. [76][c]					
		Rodrigues, et al. [77]	Pinar, et al. [79][c]					

[a] In all of the studies, various identification methods were applied to microorganisms that were first captured on culture media.
[b] These involved the sequencing of total DNA directly from cultural heritage objects without preculture.
[c] These studies used Sanger sequencing in conjunction with DGGE.Bold: Studies that used both a culture-dependant and culture-independent approach.

aspiration-based technique, that mainly collected dust deposited on the materials.

Culture-dependant approach

Culture-dependant approaches are known to characterise only 0.1–1% of the microorganisms present [2]. Only this tiny percentage of microorganisms is able to grow on cultivation media under laboratory conditions, and thus only a small portion of microorganisms can be isolated from the surface of cultural objects using these techniques [2,13]. The remaining percentage represents hitherto unknown species or species in a viable but non-culturable state (VBNC), and it is not possible to create suitable laboratory conditions for them [2]. Despite the fact that traditional culture-dependant methods do not provide complete information on the microbiological diversity on cultural heritage objects, they are still widely used, as can be seen in Table 1. In the studies listed in Table 1, various cultivable microorganisms were identified. However, the most frequent isolates included the well-known bacterial genera *Bacillus, Pseudomonas, Staphylococcus* and fungal genera *Aspergillus, Cladosporium, Penicillium*, across all types of cultural heritage objects. It is the isolation and identification of fungi that has been more frequently addressed in studies, perhaps because fungi tend to be identified as the main contaminants at most cultural heritage sites.

We would also like to mention the cultivation media used. From the studies listed in Table 1, it is clear that the most commonly used culture media for fungal cultivation are malt extract agar (MEA), Sabouraud dextrose or glucose agar, and potato dextrose agar (PDA). Several studies also included Czapek Dox agar (CZA), dichloran rose bengal chloramphenicol agar (DRBC), and dichloran glycerol agar (DG18), which is used to capture xerophilic species [128,176]. Antibiotics, such as chloramphenicol, were often added to the media to prevent bacterial growth. Similarly, nystatin or cyclohexamide were used to prevent fungal growth. Nutrient agar (NA) and tryptic soy agar (TSA) were most commonly used to capture bacteria by culture techniques.

In order to accurately estimate the microbial diversity of the studied community, the use of several different culture strategies is recommended, for instance, various incubation temperatures, pH conditions, concentrations, and types of nutrients. It is also recommended to add nutrient-poor media to the analysis, as they do not favour the growth of the fast-growing species at the expense of the slow-growing species [218]. One such nutrient-poor medium is Reasoner's 2A agar, which is suitable for slow-growing bacteria species thanks to its low nutrient concentration and a sodium pyruvate content that increases the regeneration of microorganisms exposed to stress conditions [42,219]. The use of this agar could increase the capture of bacteria from low-nutrient environments, such as stone or murals. However, this agar has only been used in five studies that are listed in Table 1, with three of them focusing on the analysis of stone objects [159,166,167], one on albumen photographs [49] and one on paper and parchment [34].

Culture-independent approach

To obtain a comprehensive overview of the microorganisms present in a given environment, metagenomics and metatranscriptomic studies are used. These studies use genetic material obtained directly from cultural heritage objects and have become increasingly popular over the last 20 years [2]. Metagenomics provides insight into the whole taxonomic profile of the microbial community, which includes living cells, VBNC cells, or even dead microbial cells. In contrast, metatranscriptomics provides information about genes that are expressed in a given environment, which makes it possible to identify only active species [164,220]. Metagenomic and metatranscriptomic studies have increased considerably with the development of NGS, which enables deeper sequencing than older methods, such as Sanger sequencing [15,221,222].

1st. generation sequencing

Sanger sequencing. Even today, the method of Sanger sequencing does not come without limitations. The major one is that only one sequencing reaction can be analysed, and therefore it is necessary to separate the DNA into individual fragments. This can be accomplished by cloning fragmented DNA from a biological sample [223]. It can be encountered quite often in conjunction with denaturation gradient gel electrophoresis (DGGE), which precedes the sequencing. More than half of the studies in Table 1 used this conjunction.

Despite this limitation, relatively outdated Sanger sequencing is still a widely used culture-independent approach in the field of cultural heritage (Table 1). Sanger sequencing in combination with cloning studies have been able to detect the presence of a variety of cultivable and non-cultivable microorganisms. As an example, we cite the study of Ma, et al. [204], which managed to capture high microbial biodiversity on the ancient wall paintings of the Mogao Grottoes. They were able to identify several bacterial and fungal species classified into 11 bacterial phyla and 3 fungal phyla. Despite the decent results obtained by this sequencing method, Sanger sequencing has been abandoned in recent years, and the most recent studies of cultural heritage thus date to 2017. This is probably due to the ever-increasing popularity of NGS and TGS techniques. These will therefore be focused on below.

NGS - 2nd generation sequencing

The 2nd generation sequencing technologies, involve massively parallel sequencing of short reads. These techniques are characterised by high-throughput, multiplexed sequencing. The multiplexing of samples significantly reduces the cost per sample [224]. NGS sequencing techniques include 4 platforms: pyrosequencing, Illumina, SOLiD, and Ion Torrent. The first NGS technology, launched in 2005 by 454 Life Science (now Roche), was pyrosequencing. A year later, the Illumina sequencing platform came to the market. In 2007, a third technology was launched, the Oligo Ligation Detection (SOLiD) sequencing method from Applied Biosystems. The last one, the Ion Torrent platform, similar to the 454 platform, was launched in 2010 by a company now known as Life Technologies [225]. Despite several years' history of NGS techniques in the field of cultural heritage, there are only a few studies available [15]. Until now, no study dealing with cultural heritage objects has used SOLiD sequencing. The Ion Torrent and pyrosequencing methods were used in a few studies, and Illumina is one of the most used NGS techniques for analysing cultural heritage objects (see Table 1 for reference).

Pyrosequencing. Pyrosequencing has proven to be a successful tool for microbial identification, but relatively short reading lengths require a careful selection of targets and placement of oligonucleotide primers [226]. Nevertheless, the pyrosequencing platform is used in a wide range of applications [227]. One of the possibilities of using this technique is the microbial screening of historical cultural objects. Pyrosequencing has already been successfully used to identify microorganisms on parchment [98], textiles [122], stone buildings [133], and murals [193,196] (Table 1).

The first of the above studies, Migliore, et al. [98] focused on parchment and reported that the main bacterial phyla were Actinobacteria and Proteobacteria (mainly Gammaproteobacteria). The phylum Firmicutes and especially its families Staphylococcaceae and Lactobacillales were also identified. In a subsequent study by Brzozowska, et al. [122] on historical textiles, the authors reported that most of the identified bacteria belonged to the phyla Proteobacteria, Firmicutes, and Bacteroidetes. More specifically, they

mention Clostridiales, Lactobacillales, and Bacillales. Cutler, et al. [133] looked at the identification of eukaryotes on the surface of sandstone buildings in Northern Ireland. They were able to identify a large number of taxonomic units, including rare taxa, specifically the four algal phyla Chlorophyta, Charophyta, Ochrophyta, and Prasinophyta. At the same time, it was also possible to identify three fungal phyla, most notably Ascomycota, Basidiomycota, and Glomeromycota.

Similar species were identified in the studies of Vasanthakumar, et al. [196] and Rosado, et al. [193], which focused on the same type of cultural monument – murals. They identified genera such as *Penicillium* or *Cladosporium* by culture-dependant methods. The pyrosequencing method allowed the authors to obtain a wider range of species and therefore culture-dependant methods were labelled as insufficient to investigate biodiversity. Pyrosequencing mainly identified the known genera *Cladosporium, Penicillium*, and *Aspergillus*. Differences can be observed in the identification of bacteria. Vasanthakumar, et al. [196] mainly mention the bacterial classes Bacilli and Actinobacteria, and Rosado, et al. [193] the bacterial species *Catenibacterium, Anaerococcus, Roseburia, Streptococcus* and many others.

In all the above-mentioned studies, pyrosequencing seems to be a good technique for microbial identification. However, pyrosequencing has its disadvantages. For example, systematic errors in reading frame and higher sequencing costs than other commercial technologies, such as Illumina Solexa [228]. These disadvantages may be the reason why not too many studies in the field of cultural heritage use pyrosequencing.

Illumina Solexa. Illumina now offers the HiSeq 2500, NextSeq 500, and MiSeq platforms. Each of these platforms is used for different applications. The first one, the HiSeq platform, is particularly suitable for sequencing the whole genome of an organism with a larger genome, such as humans. The next one, NextSeq, is used mainly for exome sequencing. The MiSeq platform is better for the *de novo* sequencing of small genomes, such as bacterial or viral, because it allows the longest read lengths [229].

The Illumina method is described as a very useful tool for metagenomic studies of microbial communities [214]. In microbial ecology studies, the MiSeq platform has become dominant thanks to its higher accuracy and longer sequence reads [230]. Illumina MiSeq is widely used to screen microbial diversity on various cultural heritage objects [43,100,214]. It has already been used for the microbial analysis of wood, written documents, audio-visual materials, stone objects, and paintings (Table 1).

There have been quite a few studies that use Illumina MiSeq sequencing. Therefore, we will not list all the results of each study here, but will only give a few examples. This method has been successful in obtaining a wide range of microorganisms across all cultural heritage objects. One example is the identification of 117 fungal genera on canvas in the study by de Carvalho, et al. [214], despite the low amount of DNA extracted. Another example is the identification of 435 species of bacteria in the study by Duan, et al. [194], or 518 species of bacteria in the one conducted by Duan, et al. [197], where both studies focused on murals. Furthermore, high biodiversity was found in the study by Szulc, et al. [43] that dealt with audio-visual materials. Next, the method has also proven to be a suitable means to observe the differences between two types of samples [32]. Last but not least, it should also be mentioned that even thousands of OTUs have been obtained in some stone monuments [135,142,149]. Considering the abundance of applications compared to other sequencing methods and especially considering the results of the studies, it can be concluded that the method is suitable for microbiological studies on all types of cultural heritage objects.

Ion torrent. In the year 2014, the Ion Torrent platform was described as the fastest NGS platform, but like pyrosequencing, it has a relatively high error rate. This could be the reason why only two studies of microbial contamination of cultural heritage have used this method to this day [225]. However, Ion Torrent has been successfully used for the analysis of marble statues [139], and a historic brick townhouse along with its paint coating [136] (Table 1).

In the first released study, the authors recommended Ion Torrent as a fast and easy way to identify bacteria and archaea with great potential [136]. It was possible to identify a total of 145 different genera in the pooled libraries for bacteria and archaea. A different composition of the microbial communities on the bricks and paint coating was demonstrated. The paint coating proved to be unsuitable for the proliferation of microorganisms, dominated mainly by the phylum Actinobacteria and its genera *Pseudonocardia, Proteobacteria* and *Acidobacteria*. In contrast, a higher biodiversity was found on the bricks. The genus *Rudobacter* (also Actinobacteria) was found to be abundant.

In the latter study, a total of 3 samples were obtained from marble sculptures and a total of 22 bacterial strains were detected. The samples were mainly dominated by Actinobacteria and the Firmicutes phylum. amongst the eukaryotes, the Ascomycota phylum was mainly dominated by the order Eurotiales (genera such as *Aspergillus, Penicillium* - both already identified as agents of rock biodeterioration). Although considerably less abundant, the Basidiomycota phylum was also identified in all samples. From this phylum, the authors listed, for example, the orders Agaricales or Malasseziales.

TGS - 3rd generation sequencing

New approaches have been developed in the last decade – they are generally referred to as third-generation sequencing or long-read sequencing [231]. The advantages of TGS are real-time data collection and, therefore the fast turnaround time. Furthermore, by using native DNA, any errors introduced during DNA amplification of short reads are eliminated. Compared to NGS techniques, these techniques bring changes to the process of preparing samples for sequencing, with only minimal library preparation steps required. TGS methods also bring limitations compared to NGS techniques, such as read accuracy. However, this is continuously improving due to advances in software analysis [224]. In this field, two technologies currently dominate: Single-Molecule Real-Time (SMRT), released in 2011 by Pacific Biosciences, which has not been used for studying cultural heritage objects yet, and Oxford Nanopore Technologies, released in 2014 [231]. However, studies that use Nanopore in the field of cultural heritage are still limited.

Nanopore sequencing. The MinION sequencer has a big advantage – it is a pocket-sized device which allows for direct on-site analysis (for example, directly in a museum or other archival facility) [215]. To this day, Nanopore sequencing and its pocket-sized sequencer MinION have already been applied in three studies of cultural heritage objects (Table 1) to observe microbial contamination on paper documents [109], stone objects [137], and oil canvas paintings [215].

In a study by Grottoli, et al. [137], the results obtained by the MinION sequencing of a stone object were compared with classical cultivation methods. The authors report that the overlap of results is very poor, probably due to the large percentage of non-culturable microorganisms. Despite the fact that this was a work focused on bacteria, several plant species were identified, which the authors explain by the fact that pollen may have been present on the analysed walls.

In the study by Pinar, et al. [215], a large number of species were identified. Two paintings in which active fungal colonisation

was visible were examined, and the differences in their biodiversity were shown. The genera *Aspergillus, Penicillium* and *Paracoccidioides* were identified on both. However, some species were only identified on one of the paintings - N (this one had a cracked varnish) and some only on the second painting – M (this one had a mouldy surface). In addition to fungi, several species of bacteria were also identified. Bacteria of the genera *Cryobacterium* and *Ralstonia* were amongst the most abundant in both. Moreover, potential pathogens such as *Mycobacterium* or *Staphylococcus* were also present. A species of *Mucilaginibacter* that can degrade xylan was also identified, but only on the first painting (N).

In the above-mentioned study by Pinar, et al. [109], high biodiversity was demonstrated on paper documents. Surprisingly, more species of bacteria than fungi were identified. The authors explain this either by the sequencing technology used or the sampling strategy chosen. The results varied between documents. It is noted that each had a very specific microbiome. In particular, the bacterial phylum Proteobacteria and its class Gammaproteobacteria were shown to dominate, but the presence of Actinobacteria or the Firmicutes phylum was also demonstrated. As far as fungi are concerned, mainly the presence of the Ascomycota phylum and, in one drawing, a Chordata phylum was demonstrated. The phyla of Basidiomycota, Mucoromycota and Microsporidia were also identified, but only in minor amounts.

In these three studies, MinION was proven to be quick and easy to use, and with somewhat lower costs than the NGS [109]. These are the main reasons why this platform has considerable potential to become a commonly used method in the field of microbial mapping of cultural heritage objects [215].

Combination of both approaches

It has been reported that culture techniques are a good tool for characterizing biodeteriogenic agents, but are inadequate for examining the overall diversity and abundance of microorganisms [193]. Therefore a combination of both approaches is the most desirable, as they are complementary, and the obtained results can provide new insight into the biodeterioration of cultural heritage objects. Thus, we obtain a complete profile of the colonizers and deal with the limitations of both techniques [144,176].

The studies (Table 1, highlighted in bold) which compared the diversity of microorganisms by both approaches revealed interesting results. Generally, more species were identified using cultivation-independent techniques, including those that are fastidious or not cultivatable at all [110,112,115,159,193]. For example, Krakova, et al. [108], describing paper biodeterioration, reported that there were only a few similarities between the results from both culture-dependant and culture-independent methods. Using the culture-dependant technique, only 12 bacterial species and 13 fungal species were identified. All these species plus many others (in total 112 bacterial and 179 fungal genera) were confirmed by Illumina MiSeq sequencing. Similarly, in a study by Rosado, et al. [164], only 38 isolates (bacterial and fungal altogether) were isolated by culture-dependant techniques, while 993 bacterial operational taxonomic units (OTUs) and 133 fungal OTUs were identified by Illumina MiSeq. Slightly different outcomes were published by Michaelsen, et al. [110] and Schroer, et al. [167]. In the former study, 5 genera were isolated using the culture-dependant method, while DGGE followed by Sanger sequencing only confirmed 3 of these and an additional 4 more genera. In the second study by Schroer, et al. [167], a total of 135 isolates were obtained by culture-dependant techniques; however, not all were confirmed by Illumina MiSeq sequencing. Therefore, their combination can lead to capturing more diversity.

Furthermore, the combination of both approaches (Table 1, highlighted in bold) gives the possibility of not only focusing on the diversity of contaminating microorganisms, but also on their physiology and metabolism [14,137] or on specific enzyme activities which play a crucial role in the biodeterioration of cultural heritage objects. The most commonly monitored include cellulolytic activity [217], proteolytic, catalase and peroxidase activities [49], lipolytic activity [166], and ligninolytic and cellulolytic activities [85,89]. In all these cases, special media containing the substance which is cleaved by the monitored enzyme were used. The other option is the usage of specific kits that allow the detection of the entire spectrum of enzyme activities at once. One of these is the API Zym® system for observing up to 19 enzymes, which was used in the studies by Lopez-Miras, et al. [68,216]. Although enzyme activities have not been investigated in many studies combining both approaches, their monitoring provides additional essential information about the microorganism burden and biodeterioration of cultural heritage objects.

Conclusion

Despite all the efforts of conservator-restorers and historians to ensure proper storage conditions, current knowledge is still insufficient to protect historical objects [4]. The most important is to prevent all possible defects and calamities, which can affect further contamination. However, some faults/accidents may still occur, and long-term appropriate storage conditions may be compromised or not maintained at all. These events facilitate the microbial colonisation of materials and their subsequent biodeterioration. In these situations, is important to identify the causes of contamination, determine their consequences, identify the most sensitive cultural heritage materials for biodeterioration and target an effective disinfection method.

As our review shows, over time microorganisms can colonise and degrade any cultural heritage object. Depending on the environmental conditions and chemical properties of the object, chemoorganotrophic, chemolithotrophic, or photolithotrophic microorganisms can dominate [232]. Nevertheless, it is essential to simultaneously identify the microbial populations present and their biochemical processes that may be involved in causing damage [13].

To the best of our knowledge, this review presents all studies that deal with the microbial biodiversity of discussed cultural heritage objects in 2005–2021. It has been shown that even after 16 years of NGS methods, studies using culture-dependant techniques and the obsolete Sanger sequencing still predominate. This is probably due to the still high financial costs of NGS or the problematic evaluation of the bioinformatics data obtained by NGS. It was also observed that the presented studies usually do not specify which of the identified microorganisms are the ones responsible for biodeterioration. Thus, there is a lack of a proposal for a disinfection or prevention method to target certain microbial species occurring on the materials, which is necessary to save cultural heritage objects for future generations. In addition, microbial contamination carries a risk not only for cultural objects, but also for the employees of archives and museums. In fact, the inhalation of fungal spores can cause respiratory disorders which pose a significant health risk [29]. Therefore, it is appropriate to include air analysis in the studies.

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