Review

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Abstract: This review resumes published data on fungal diversity in and within monuments (e.g., religious and secular monuments, museums, and statues), covering a multidisciplinary investigation into the complex interactions between fungi and cultural heritage structures. Fungi represent remarkable adversaries to monuments, potentially compromising their structural integrity and aesthetic value. Based on a bibliographic search of manuscripts published, the knowledge of fungal communities colonizing monuments was comprehensively assessed. This work first describes the diverse fungal species implicated in the degradation of monument materials (e.g., stone, metal, and glass). It elucidates the factors governing fungal colonization and proliferation in and within these structures (e.g., environmental conditions, construction materials, and human interventions). Finally, the efficacy of preservation and restoration techniques to mitigate fungal threats and safeguard our cultural heritage is also discussed. This synthesis highlights the pivotal role of mycological research in heritage conservation, and a platform for future studies to address critical knowledge gaps is provided. Understanding fungal diversity in and within monuments is critical to preserving these invaluable cultural treasures, as it informs targeted conservation strategies and ensures their longevity in the face of fungal challenges.

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1. Introduction

According to the United Nations Educational, Scientific and Cultural Organization (UNESCO), heritage is the legacy from the past, what we live with today, and what we pass on to future generations, that constitutes irreplaceable sources of life and inspiration [1]. Therefore, the total or partial destruction of a country's heritage is the denial of its identity, comparable to attacks on freedom of thought, conscience, and religion [2].

Heritage includes natural and cultural or historical monuments. Natural monuments include natural places, characterized by their natural beauty or outstanding biodiversity, ecosystem, and geological values (e.g., East Africa's Serengeti, the Great Barrier Reef in Australia) [3,4]. Cultural or historical monuments includes artefacts, monuments, buildings and sites, museums with symbolic, historic, artistic, aesthetic, ethnological or anthropological, scientific, and social value (e. g., the Pyramids of Egypt or the Great Wall of China) [4,5] (Figure 1).

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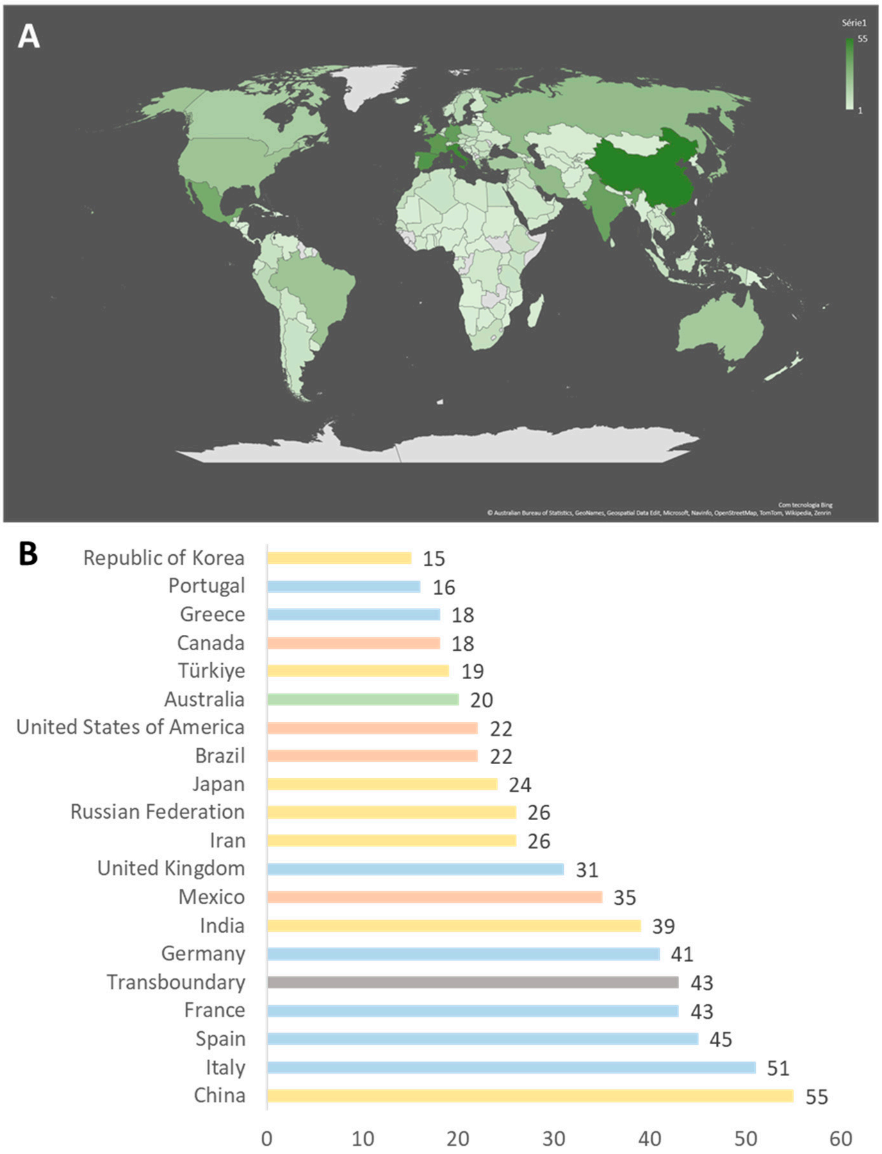

Figure 1. World heritage, including cultural, natural, and mixed sites, distributed by country (A) and list of the countries with higher concentration of heritage sites (B) (adapted [4]).

The architectural marvels that constitute these cultural or historical monuments, intaglio with artistic finesse and plentiful in historical context, must be recognized not as silenced edifices but as living repositories of our collective heritage [6]. Since forgotten ages, these monuments represent human virtues such as creativity, perseverance, friendship, love, and hope [7]. The resounding echoes of history, culture, and art within these structures make them invaluable treasures.

Four days after the beginning of the war against Ukraine, the Ivankiv Regional History Museum and part of its collection (Maria Primachenko paintings) were lost due to an attack perpetrated by the Russian troops. After this initial attack, the world witnessed the destruction of 289 Ukrainian cultural heritage sites (i.e., 120 religious sites, 27 museums, 109 buildings of historical or artistic interest, 19 monuments, 13 libraries, and one archive) have been destroyed (Figure S1) [8].

Also, on September 2, 2018, the fire at the National Museum of Brazil affected this historic building located at the Boa Vista Park, in Rio de Janeiro. This incident almost destroyed the historical collection, accumulated in around two hundred years, and which had become one of the oldest in the world [9].

Nevertheless, a more insidious and subtle threat lurks within their foundations: diverse fungal colonies that inhabit these monuments. Fungi (yeasts, molds, mushrooms, and toadstools), often inconspicuous and underestimated, infiltrate these monuments, carving their presence into the

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materials composing these edifices [10–12]. Studying fungal diversity within cultural and historical monuments cannot be overstated. Fungi are not merely passive bystanders; they are active participants in the aging and degradation of these structures [13,14].

This work aims to emphasize the relevance of fungal diversity to monument preservation and conservation, discuss factors influencing fungal diversity, evaluate the potential impact of fungal diversity on monument degradation and structural integrity, revise the role of mycological research in monument management, and highlight the importance of a multidisciplinary approach involving mycologists and heritage conservation experts.

2. Monuments

This section focuses on historical and cultural monuments. Herein, the different types of religious and secular monuments and other pieces of artistic and architectural interest are described, and examples are presented.

2. 1. Religious Monuments

Churches and cathedrals are used as places of congregation for believers and practice religious ceremonies by the Christian Faith (i.e., Catholic, Protestant, Orthodox, or Anglican) [15]. Built under different architectural styles - from Romanesque to Post-modernism, they reflect the evolution of religious and artistic sensibilities [16]. (e.g., the Notre-Dame Cathedral in Paris, France, and the Saint-Sophia Cathedral in Kyiv, Ukraine).

The Islamic Faith uses mosques to gather prayers, conduct religious ceremonies, and study Islamic teachings [17]. Built according to a simple and functional architectural design, they possess a prayer hall facing the qibla (Mecca's direction) and a minaret to call to prayer (adhan) [18], and the interiors are decorated with calligraphy and geometric motifs [19] (e.g., the Hagia Sophia in Istanbul, Turkey, and the Al-Aqsa Mosque in Jerusalem, Palestine).

For many worldwide belief systems, temples and shrines are places of worship where religious ceremonies occur and community gathers (e.g., Judaism, Buddhism, Hinduism, Shinto). Often housing religious idols, symbols, and artefacts, these structures are used for veneration, prayer, and offerings to deities, ancestors, or spirits [20] (e.g., the Angkor Wat in Siem Reap, Cambodian, and the Ise Grand Shrine in Ise, Japan).

2.2. Secular Monuments

Palaces, associated with royalty and nobility, episcopate, or heads of state, serve as residences, administrative centres, and symbols of authority (e.g., the Palace of Versailles in Versailles, France, and the Alhambra in Granada, Spain) [21].

Castles, fortified structures primarily designed for defensive purposes, present walls and towers and are strategically positioned. Historically, these structures were used as military strongholds to protect against invaders [22] (e.g., the Neuschwanstein Castle in Bavaria, Germany, and the Himeji Castle in Himeji, Japan).

Government buildings are constructed to serve as government administrative, legislative, or executive centres. They house public officials and civil servants to carry out governance-related duties, policy-making, and public service [23] (e.g., the Capitol in Washington, D.C., USA, and the Palace of Westminster in London, England).

2.3. Cultural and Knowledge Institutions

Museums collect, preserve, exhibit, and interpret objects, artefacts, artworks, and specimens with cultural and artistic (art museums), historical (history museums), and scientific or educational significance (science or natural history museums). Besides serving as repositories of human knowledge and creativity, they provide opportunities for public engagement, learning, and appreciation of the past, present, and future [24] (e.g., the Louvre in Paris, France, and the Metropolitan Museum of Art in New York, USA).

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Cultural centers are institutions, venues, or spaces dedicated to promoting, preserving, and celebrating culture, arts, heritage, and education. These institutions are hubs for cultural activities, including exhibitions, performances, workshops, lectures, and community events. Also, they focus on specific cultural groups, art forms, or interdisciplinary approaches, allowing cultural understanding and appreciation [25] (e.g., the Japan Cultural Institute in Paris, France, and the National Hispanic Cultural Center in Albuquerque, USA).

Libraries house curated collections of books, periodicals, digital resources, and other materials organized and available for public access, study, research, and borrowing. As educational and cultural institutions, they provide resources, services, and spaces for learning, reading, and intellectual exploration, promote literacy, access to information, and knowledge dissemination [26] (e.g., the Library of Congress in Washington, D.C., USA, and the Vatican Library in Vatican City).

2.4. Monumental Artefacts

Memorials, including statues, plaques, gardens, museums, and architectural landmarks, evoke expressions of the collective memory and remembrance and provide constituting places for reflection, tribute, and recognition [27] (e.g., the 9/11 Memorial in New York, USA, and the Holocaust Memorial in Berlin; Germany).

Statues, three-dimensional representational objects depicting people, animals, mythological figures, or objects, are created to honor or commemorate a specific individual, event, or concept [28]. Compared to statues, sculptures encompass a broader range of three-dimensional artistic expressions, including abstract and non-representational works created for diverse aims, such as decorative pieces or conceptual purposes beyond honoring specific individuals or events [29] (e.g., the Statue of Liberty in New York, USA, and the Great Sphinx in Giza, Egypt).

Monoliths are large, single stones or rock formations standing upright. These structures can naturally occur as large standing stones or columns or be arranged by humans for specific purposes as megalithic monuments or artistic installations [30] (e.g., Stonehenge in Wiltshire, England, and Ahu Tongariki in Easter Island, Chile).

Obelisks are tall, narrow, four-sided monuments with a pyramidal top. Used since ancient civilizations, such as Egyptians, these structures were regarded as symbols of power or religion or as commemorative markers. Typically made from a single stone piece, they were carved with inscriptions and decorative motifs [30] (e.g., the Cleopatra's Needle in London, England, and the Washington Monument in Washington, D.C., USA).

2.5. Bridges and Aqueducts

Built to span gaps (i.e., rivers, ravines, or roads), bridges provide a pathway for vehicles, pedestrians, and trains. These structures are designed according to specific needs and geographic conditions, including arch bridges, suspension bridges, cable-stayed bridges, and beam bridges [31] (e.g., the Golden Gate Bridge in San Francisco, USA, and the Tower Bridge in London, England).

Aqueducts are engineered channels, tunnels, or conduits that transport water from the spring to a given destination. Historically, these structures have supplied cities and agricultural areas with reliable water [31] (e.g., the Pont du Gard in Vers-Pont-du-Gard, France, and the Segovia Aqueduct in Segovia, Spain).

2.6. Fountains and Water Structures

Fountains are decorative water elements that include a central water source, such as a jet or spout, that expels water that returns to a basin or pool. Simple or more elaborate, they can be found in public squares, parks, gardens, and private estates [32] (e.g., the Trevi Fountain in Rome, Italy, and the Fountain of Wealth in Suntec City, Singapore).

Water structures include architectural elements that have water as a critical component, such as ponds, pools, canals, cascades, waterfalls, and aqua gardens. These structures can be incorporated into landscapes, architectural designs, and urban planning to create environments that are serene and

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aesthetically pleasing [33] (e.g., the Gardens of Versailles in Versailles, France, and the Alhambra Generalife Gardens in Granada, Spain).

3. Materials Used for Building and Decoration

The choice of materials used for construction and decoration defines the characteristics of structural integrity and aesthetic value. The present section delves into the materials used for building and decoration and provides examples of monuments using these materials (Table S1) [34].

3.1. Building materials

- Stone:

Due to its durability, strength, versatility, and aesthetic value, stone has been the preferred choice for constructing monuments and structures throughout history. This material has been used since the Prehistoric Period (Before 10,000 BCE) for building shelters, walls, fortifications, or megalithic structures. The most common types of stone used by artists over time have been marble and limestone, of the calcareous type, and granite, of the siliceous type [35].

Marble is a metamorphic rock mainly composed of calcite ($CaCO_3$) minerals. Frequently used for its beauty, translucency, and ability to be polished, it is considered the material of excellence for architecture (as building material) and plastic arts (in floorings, statues, and other decorative elements). In terms of color, it can be monochromatic (white, cream, red, pink, black, yellow) or polychromatic (made up of several colors, given by the veins or fragments that form part of the stone) [36] (e.g., the Parthenon in Athens, Greece, and David by Michelangelo).

Limestone, a sedimentary rock mainly composed of calcium carbonate ($CaCO_3$) in the form of calcite or aragonite, magnesium carbonate (dolomite), and other minor constituents, such as clay, iron carbonate, feldspar, pyrite, and quartz. Being relatively soft and easy to carve, this stone is ideal for architectural details and sculptures. This stone presents several colors, from white to beige and grey [37] (e.g., the Chartres Cathedral in Chartres, France, and the Great Sphinx in Giza, Egypt).

Granite is an igneous rock composed of feldspar, quartz, mica, and smaller quantities of other minerals (e.g., hornblende, biotite, and pyroxene). Characterized by its hardness, durability, and elevated resistance to erosion and weathering, it has been commonly used for structural elements, such as columns and facades. Granite's colors range from pink to grey and black [38] (e.g., the Mount Rushmore National Memorial in South Dakota, USA, and the Avukana Buddha Statue in Sri Lanka).

- Wood

Due to its excellent mechanical properties, lightweightness, and easiness of shape, timber has remained a primary construction material since prehistoric times [39]. Some types of wood used for monument construction and decoration will be presented.

Oak (*Quercus* spp.), a hardwood, is notorious for its strength, durability, and resistance to decay [40,41]. This wood is often used for flooring, furniture, cabinetry, and other decorative elements (e.g., the Hall of Mirrors in the Palace of Versailles, France).

Black cherry (*Prunus serotina*), belonging to the same group, is moderately heavy, strong, stiff, and hard and presents high resistance to shock. This wood is frequently employed for furniture, moldings, and cabinetry [40,41] (e.g., the Shaker Village of Pleasant Hill in Kentucky, USA).

Maple (*Acer* spp.), another hardwood, is resistant to shock and has high shrinkage. This wood is frequently used for flooring, furniture, cabinetry, and interior details [40,41] (e.g., the Maple Leaf Gardens in Toronto, Canada).

Cedar (including *Chamaecyparis* app, *Juniperus* spp., and *Thuja* spp.), a softwood, is moderately lightweight, stiff, strong, and hard, known for its resistance to decay, insects, and rot. In monuments, it is applied for doors, roofing, and decorative details [40,41] (e.g., the Cedar Shingle Mill at Old Sturbridge Village, Massachusetts, USA).

Pine (*Pinus* spp.), belonging to the same group, constitutes an affordable choice for construction. Although not as durable as hardwoods, it can be treated and used for framing, sheathing, and interior woodwork [40,41] (e.g., the Old North Church in Boston, USA).

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Redwood (*Sequoia sempervirens*), a softwood, is durable and naturally resistant to insects and decay. It is used in doors, siding, and structural elements [40,41] (e.g., the Ahwahnee Hotel in Yosemite National Park in California, USA).

Teak (*Tectona grandis*), belonging to the group of exotic hardwoods, is characterized by its durability and resistance to moisture and insects. It is used for carvings, panels, and outdoor elements, especially in regions with high moisture levels [40] (e.g., the Phra Thinang Dusit Maha Prasat Hall at the Royal Palace of Bangkok, Thailand).

Mahogany (*Swietenia macrophylla*), another exotic hardwood, is frequently used for architectural details, carvings, furniture, cabinetry, and other decorative elements [40,41] (e.g., the Mahogany Bay Village in Belize).

- Metal

The long history of using metals in construction began in the Ancient Civilizations - the Sumerians and Egyptians used bronze in tools and decorative elements, while the Hittites and Assyrians used iron for construction elements, including structural beams, nails, and tools.

Bronze, a copper and tin alloy, is known for its durability, corrosion resistance, and attractive patina. This metal can be used for casting plaques, statues, and sculptures [42] (e.g., the Statue of Liberty in New York, USA, and the Little Mermaid in Copenhagen, Denmark).

Iron is frequently used as a structural component of bridges and industrial-era buildings or as a decorative detail with ornate designs in gates, railings, and balconies [43] (e.g., the Eiffel Tower in Paris, France, and the French Quarter in New Orleans, USA).

Steel, an iron and carbon alloy, is a versatile and robust material widely used in structural components, frameworks, and support systems [44] (e.g., the Gateway Arch in Missouri, USA, and the Atomium in Brussels, Belgium).

Copper, appreciated for its natural beauty and corrosion resistance, has been used for roofing, cladding, and decorative elements [45] (e.g., the top of the Washington Monument in Washington, D.C., USA, and the Museum of Fire in Żory, Poland)

Stainless steel is an alloy containing at least 10.5% chromium and usually other elements (e.g., nickel, molybdenum, titanium, aluminum, niobium, copper, nitrogen, sulfur, phosphorus, or selenium). This alloy, known for its high corrosion resistance, is commonly used for structural components, cladding, and sculptures [46] (e.g., the Cloud Gate sculpture in Millennium Park in Chicago, USA, and the One World Trade Center in New York City, USA).

Aluminum, a lightweight metal, presents excellent corrosion resistance. It is suitable for structural components, facades, and modern architectural designs [47] (e.g., the Winged Anteros at the top of the Shaftesbury Memorial Fountain in Piccadilly Circus in London, England, and the Christ the Redeemer statue in Rio de Janeiro, Brazil).

Lead, recognized for being highly durable and corrosion-resistant, is used for roofing and ornamental details in traditional architecture [48] (e.g., the roof of the Lincoln Memorial in Washington, D.C., USA).

Gold leaf, made from thin sheets of gold, is used for gilding architectural details and sculptures [49] (e.g., the Golden Temple in Amritsar, India, and the dome of the Bahai Temple in Haifa, in Israel).

- Glass

Glass, mainly composed of silica (provided by sand) and fluxing agents (e.g., ashes of plants, trees, and bracken), is a versatile building material used for its transparency, aesthetics, and functional properties [50]. Herein, different types of glass used in monuments, along with examples where it has been incorporated, are presented.

With a characteristic circular pattern and relatively good optical quality, crown glass is made by blowing a large glass bubble and flattening it. Widely used in the 18th and 19th centuries, this type of glass has been used in windows of ancient monuments [51] (e.g., the Crown Glass Windows in St. Mary's Church in Fairford, England).

Stained glass, a decorative glass often used in monuments and buildings, creates intricate and colorful designs of light and color. During manufacturing, metallic salts are added to molten glass, producing various colors. The glass is then cut into small pieces and assembled to form patterns,

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images, or scenes [52] (e.g., the stained glass of Notre-Dame Cathedral in Paris, France, and the Sagrada Família in Barcelona, Spain).

Glass mosaics, small colored glass pieces - glass *tesserae* - are used to create intricate and detailed designs or patterns in wall coverings, flooring, or other decorative elements [53] (e.g., the Hagia Sophia in Istanbul, Turkey, and the Temple of the Reclining Buddha in Bangkok, Thailand).

- Clay-based ceramics

Clay-based ceramics are amongst the oldest, being used since Ancient Mesopotamia (around 4000 BCE), they are the most versatile materials used in construction. These ceramics differ in chemical composition, properties, and applications [54].

Bricks are made of clay, shale, or a combination of both, molded into shape, dried, and fired at high temperatures in a kiln. Bricks are molded in different shapes and sizes and present diverse colors according to their composition. When laid in various patterns, it is possible to create decorative facades. Due to their durability, versatility, and ease of manufacturing, bricks are commonly used for walls, arches, and structural elements [55] (e.g., the Great Wall of China and the Red Fort in Delhi, India).

Terracotta, meaning "baked earth" in Italian, is made from clay that is more refined than the clay used in bricks, resulting in a less dense and more porous material with a distinctive reddish-brown color. Terracotta is commonly used for decorative purposes, such as architectural details, sculptures, ornamental facades, and pottery [56] (e.g., the Terracotta Army in China's Qin Shi Huang Mausoleum and the Roof of the Watts Towers in Los Angeles, USA).

- Concrete

Concrete results from the combination of cement, water, aggregates (e.g., sand, gravel, or crushed stone), additives, and admixtures. This material is known for its strength, durability, processability, adaptability, and low-cost, concrete and has been a popular choice in construction over the last 200 years [57,58] (e.g., the Hoover Dam on the Colorado River, Arizona and Nevada, USA, and the Sydney Opera House in Australia).

3.2. Decorative Arts

Decorative arts are objects and artworks specially created with functional and aesthetic purposes. These items are frequently used to enhance monuments' beauty, historical authenticity, and cultural significance of living spaces. Thereafter, some of these materials will be described.

- Paintings and Frescoes

Paintings are artworks created by applying paint onto a canvas or wood that decorate walls and ceilings or be displayed as standalone art pieces [59] (e.g., Mona Lisa by Leonardo da Vinci and Kiss by Gustav Klimt).

Frescoes apply watercolor pigments to wet plaster, creating durable and long-lasting murals, which are found decorating the ceiling and walls of historical and religious monuments [60] (e.g., the Frescoes of Pompeii, Italy, and the Sistine Ceiling of the Chapel in Vatican City).

- Tapestry

Tapestry, a textile art form where designs or scenes are woven into a fabric, is often used to cover walls or as decorative hangings in monuments. Tapestries are made from different materials, such as wool, silk, cotton, and synthetic fibers. Historically, they have been used as insulation in grand palaces and homes to add warmth and style to interior spaces [61] (e.g., the collection of tapestries at the Château de Chenonceau, France, and the Cloisters in the Metropolitan Museum of Art in New York, USA).

- Furniture

Furniture is movable items designed for several purposes that support human activities such as seating, storage, seating, sleeping, and working, among other uses. In monuments, despite its practical applications, historical or ornate furniture can be used to enhance the beauty of the interior design. [62] (e.g., the furniture at the Palazzo Pitti in Florence, Italy, and the furniture at the Hampton Court Palace in London, England).

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- Other elements

Other decorative arts include ceramics and pottery (e.g., vases, bowls, plates, and figurines with intricate designs, glazes, and patterns), textiles (e.g., embroidered textiles, quilts, rugs, and lacework), glassware (e.g., stained glass windows, decorative glass vases, and glass sculptures), metalwork (e.g., iron gates, brass lamps, silverware, and cutlery), woodworking (e.g., ornate frames, wooden sculptures, and inlaid furniture), porcelain and china (e.g., dinnerware sets, teapots, and figurines), jewelry (e.g., ornamental pieces made of precious metals and gemstones), clocks and timepieces (e.g., antique and ornate clocks), decorative mirrors (e.g., framed mirrors), and bookbinding (e.g., book covers and bindings).

4. Fungal species associated with monument degradation

Biodeterioration is a geophysical and geochemical process driven by biological organisms (e.g., bacteria, cyanobacteria, fungi, lichens) inducing undesirable physical, chemical, mechanical, and aesthetic modification and damage to historic monuments and artworks [63]. Fungi are chemoheterotrophic organisms, ubiquitous in almost all environments (air, soil, water). These microorganisms play critical ecological roles as decomposers (biogeochemical cycling of the elements), symbionts, pathogens, or associated with the spoilage of natural and manufactured materials. This ability to actively participate in biogeochemical cycles allows fungi to constitute biodeterioration agents of several building materials [64].

The effects of fungi in the biodeterioration of building materials have been a well-known phenomenon since ancient times, being even mentioned in the bible as the "leprosy" or "fretting" on brick, clay, and wood (Old Testament, Third Book of Moses, chapter 14, verses 33–57) [64]. Several fungal species can contribute to this problem, compromising building and decorative materials preservation and maintenance and cultural heritage. These fungi colonize various materials and surfaces, accelerating their decay (Table S1). Understanding the fungal species associated with the deterioration of these materials is essential for effective preservation strategies.

Fungal species associated with stone surface deterioration, referred to as "stone-inhabiting fungi" or "building mycobiota, do not actively break down the mineral components of stone materials but indirectly contribute to its degradation through several mechanisms. Stone is colonized by epilithic (settling in stone surface), chasmolithic (settling in stone crevices and fissures), and endolithic fungi (settling some millimeters or centimeters into the rock pore) [65]. For instance, these microorganisms produce organic acids and enzymes that erode stone, making it more susceptible to physical weathering processes like freeze-thaw cycles and chemical weathering from acid rain. The dominant fungal species associated with stone deterioration include *Alternaria* spp., *Aspergillus* spp., *Aureobasidium* spp., *Cladosporium* spp., *Curvularia* spp., *Devriesia* spp., *Epicoccum* spp., *Fusarium* spp., *Mucor* spp., *Paecilomyces* spp., *Penicillium* spp., *Phoma* spp., and *Rhizopus* spp., *Talaromyces* spp., and *Trichoderma* spp. accompanied by lichen-forming fungi can be identified [64–89]. Visible signs of stone deterioration are surface etching, pitting, staining, discoloration, the formation of black or greenish biofilms, and surface roughening and erosion [90]. These alterations are related to acid production and excretions by fungal species. De la Torre and co-workers [91] reported that large quantities of oxalic, citric, and gluconic acids were produced by *P. frequentans* in broth cultures. These metabolites caused extensive deterioration of clay silicates, micas, and feldspars (from sandstone and granite), and also to calcite and dolomite (from limestone), resulting in high cation release and organic salts formation, such as calcium, magnesium, and ferric oxalates and calcium citrates. Comparatively, the biodegradative effect of *C. cladosporoides* was less significant since no organic acids nor organic salts were produced.

Fungal species associated with wood deterioration, called wood-decaying fungi, produce enzymes that break down the wood's cellulose and lignin into simpler compounds like carbon dioxide and water used as nutritional sources [92]. This decomposition process leads to the weakening and eventual failure of wooden structural elements in buildings or their decorative elements used as decoration [92]. Some fungal species associated with wood deterioration include *Antrodia* spp., *Athelia* spp., *Botryobasidium* spp., spp., *Cladosporium* spp., *Coniophora* spp., *Donkioporia*

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spp., *Gloeophyllum* spp., *Hyphoderma* spp., *Hyphodontia* spp., *Meruliporia* spp., *Penicillium* spp., *Pharenochaete* spp., *Postia* spp., *Mucor* spp., *Serpula* spp., *Trametes* spp., and *Trichoderma* spp. [93–107]. Species of the ascomycete *Chaetomium* can degrade various polymers and are often found growing on cellulose-containing substrates [108]. Color, texture, and structural integrity changes are visible signs of wood deterioration. In advanced stages, the growth of fruiting bodies (mushrooms) or mycelium on the wood surface may also be observed [109].

Fungal species associated with metal surface deterioration, referred to as "microbiologically influenced corrosion" (MIC), contribute to metal degradation by producing compounds, like exopolymers and organic acids, that create a more favorable microenvironment for corrosion [110]. Some common fungal species associated with metal degradation include *Aspergillus* niger, *Aureobasidium pullulans*, *Cladosporium* spp., *Hormoconis resinae*, and *Penicillium* spp. [110–115]. Visible signs of metal deterioration are the formation of biofilms, pitting corrosion, general corrosion, darkening, and staining [109].

Fungal species associated with glass deterioration are less common than those affecting wood or stone. Although fungi do not actively degrade glass, their metabolic activities can indirectly affect its appearance [116]. Some fungal species associated with glass deterioration include *Alternaria* spp., *Aspergillus* spp., *A. pullulans*, *Cladosporium* spp., and *Penicillium* spp. [117–122]. Visible signs of glass deterioration are staining or discoloration, irregular patterns or spots, and the formation of biofilms [109].

Fungal species associated with brick and terracotta surface deterioration typically colonize the porous surface of these materials. Fungi metabolic activity (e.g., production of organic acids and mycotoxins) and biofilm formation create conditions conducive to changes in their appearance [123]. Some fungal species associated with glass deterioration include *A. niger*, *A. pullulans*, *Chaetomium* spp., *Cladosporium* spp., *Penicillium* spp., and *Stachybotrys chartarum* [124]. Visible signs of brick deterioration are staining or discoloration, irregular patterns, and pigmentation production [109].

Fungal species associated with concrete deterioration, designated as "microbial-induced concrete corrosion" [125,126], produce organic (e.g., citric acid, oxalic acid, lactic acid) and inorganic acids, enzymes, and metabolic other products that react with the calcium in the concrete, weakening it and leading to surface degradation [127,128]. Some fungal species commonly associated with the deterioration of concrete include *Alternaria* spp., *Aspergillus* spp., *Aureobasidium pullulans*, *Cladosporium* spp., Fusarium spp., *Trichoderma* spp., *Mucor* spp., *Penicillium* spp., *Phoma* spp., and *Rhizopus* spp. [129–132]. Visible signs of degradation typically include surface discoloration, pitting, cracking, and fungal growth [109]. Despite causing the artwork's biodeterioration, some of these fungi also induce health concerns in personnel's health working and visiting monuments [133].

Fungal species associated with the deterioration of paintings and frescoes pose a significant threat to these artworks, potentially causing irreversible damage. Fungi can colonize paint layers (pigment solubilization capacity) and the support structure. Some fungal species associated with the deterioration of paintings and frescoes include *Alternaria* spp., *Aspergillus* spp., *Chaetomium* spp., *Fusarium* spp., *Memnoniella* spp., *Myrothecium* spp., *Neurospora* spp., *Penicillium* spp., *Scopulariopsis*, *Stachybotrys* spp., and *Stemphylium* spp. [134–157]. Visible signs of fungal colonization on paintings and frescoes are staining, discoloration, fungal growth, and structural damage to paint layers or support materials [109].

Fungal species associated with the deterioration of tapestries and textiles cause significant damage to these materials [159]. Fungi colonize the textile fibers, degrading cellulose, and other organic components, leading to material weakening and degradation. Some fungal species associated with the deterioration of tapestries and textiles include *Alternaria* spp., *Aspergillus* spp., *Chaetomium* spp., *Cladosporium* spp., *Gymnoascus* spp., and *Penicillium* spp. [159–161]. Visible signs of fungal colonization on tapestries and textiles are staining, discoloration, fungal growth, and structural damage to the fibers [109]. The spacesuits used in Apollo lunar missions (1968 – 1972), preserved at The United States Smithsonian Institution’s National Air and Space Museum, have been degraded by *Paecilomyces* sp. and *Cladosporium* sp., being observed the degradation of the synthetic polymers,

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development of fungal hyphae on individual fibers of the cloth, and the deterioration of interior layers [162].

Fungal species associated with the deterioration of books and archival manuscripts pose a significant threat to preserving these repositories of human knowledge and history [163]. Several fungal species secrete cellulolytic enzymes and organic acids that degrade cellulose and other paper components. Some of the fungal species associated with paper degradation include *Alternaria* spp., *Aspergillus* spp., *Chaetomium* spp., *Cladosporium* spp., *Fusarium* spp., *Mucor* spp., *Penicillium* spp., *Stachybotrys* spp., *Rhizopus* spp., and *Trichoderma* spp. [163–182]. Visible signs of fungal colonization on books and archival manuscripts are discoloration, staining, paper weakening, powdery mold, and a musty odor [109].

5. Factors influencing fungal colonization and proliferation

Factors affecting fungal colonization and proliferation in monuments are diverse, complex, and often interdependent. Understanding these factors is critical to preserving cultural and historical monuments' integrity and aesthetic value [183]. This section focuses on key factors influencing fungal colonization and monuments' proliferation.

5.1. Moisture

High moisture content and elevated humidity levels (> 80% RH) provide an ideal environment for fungal growth [184–186]. When these levels are elevated, fungal spores are activated and germinate, and hyphae begin their development, initiating colonization [187]. During fungal growth, the mycelium secretes enzymes and organic acids that facilitate the degradation of organic materials [188]. Moreover, moist conditions promote fungal sporulation activity [189], producing spores that can easily become airborne and spread to other parts of the monument or nearby monuments [190].

5.2. Temperature

Temperature also significantly impacts fungal proliferation in monuments. Different fungal species have specific optimal temperature ranges for growth and deviations from these ranges affect the fungal ability to colonize and deteriorate monument materials. For instance, mesophilic fungi grow best at moderate temperatures (20-30°C), psychrophilic fungi prefer colder conditions (0-20°C), and thermophilic fungi thrive at higher temperatures (above 45°C) [191].

Also, temperature and moisture levels are interconnected. Warmer temperatures can increase the capacity of air to hold moisture, leading to higher humidity within monument structures. Elevated levels of humidity, in combination with warm temperatures, create an ideal environment for fungal growth. In tropical climates, the harmful effects are maximized by high values of temperature and relative humidity prevailing during most of the year [108].

5.3. Material characteristics

Some intrinsic characteristics of the materials may either facilitate or inhibit fungal growth. One of these characteristics is nutrient availability. Organic materials, such as wood, textiles, and organic pigments used in paintings and frescoes, provide nutrients (e.g., cellulose, lignin, and starch) to sustain fungal growth and colonization; while inorganic materials like stone, metal, and glass are less susceptible to these processes [192–194].

Materials' porosity and texture also influence fungal colonization. Porous materials, including many types of stone and terracotta, provide niches for fungal spores to be deposited, offering more opportunities for fungal hyphae to establish themselves and form fungal colonies [195].

The ability of materials to absorb and retain moisture affects the efficiency of fungal colonization. Materials with high moisture absorption rates, such as wood, are more prone to fungal growth when exposed to high humidity or moisture [196].

Finally, some materials possess natural resistance to fungal attack. For instance, certain types of wood, such as cedar, produce natural compounds that inhibit fungal growth [197].

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5. 4. Microenvironment

Microclimatic conditions around monuments can differ from the surrounding environment, affecting fungal growth. Factors such as airflow and ventilation, sunlight exposure, and proximity to vegetation can influence microclimates [198,199]. Adequate airflow and ventilation prevent moisture condensation, reducing the risk of fungal colonization [200–203]. Sunlight exposure presents a drying effect of sunlight that, coupled with ultraviolet (UV) radiation, inhibits fungal spore germination [204,205]. Fallen leaves, pollen, and organic matter in the areas surrounding monuments act as reservoirs of fungal species [206], releasing spores that are introduced into monument surfaces by air movements and visitor traffic.

4.6. Pollution and Contaminants

Air pollution, particularly sulfur dioxide (SO2) and nitrogen oxides (NOx:) emissions, reacts with moisture in the air to form sulfuric (H2SO4) and nitric acids (HNO_3) [207]. These acids damaged material surfaces, forming additional niches for fungal spores' deposition and growth [208,209]. Soot and particulate matter contain organic contaminants, such as oil residues or organic waste [210], that introduce additional nutrients, favoring fungal growth; while others, such as heavy metals (e.g., Cd, Mn, or Zn), interfere with fungal metabolic processes and have toxic effects on fungal growth [211].

Urbanization has led to rapid changes in the climate, air and ground temperatures have increased in urban areas compared to their surroundings - the urban heat island effect – caused by increased heat absorption by pavement and buildings and increased heat production by air-conditioners, traffic, and factories. In general, urban heat islands are characterized by higher minimum, average, and maximum temperatures. Urban heat islands have been exerting evolutionary pressure on organisms for at least 50 years and for more than 100 years in some cities [212–214].

5.7. Historical Factors:

Previous treatments, conservation efforts, and restoration practices have profoundly impact fungal colonization, altering the composition of the communities inhabiting monument surfaces [215]. Despite being essential for heritage preservation, these interventions may facilitate fungal growth and dispersion when inadvertently performed. Among the most sensitive treatments are moisture management, removing biological growth, applying biocides and fungicides, cleaning, and surface alterations, introducing restoration materials, and using sealants and protective coatings [216].

6. Preservation and restoration techniques

Preservation and restoration techniques are critical to limit and revert the effects of fungal action and ensure the long-term survival of historical artifacts and iconic landmarks. The methods for preserving and restoring monuments impacted by fungal degradation include several steps.

6.1. Prevention and Environmental Control:

Maintaining stable environmental conditions within and around the monument is crucial since fluctuations in these parameters create ideal conditions for fungal growth. High humidity levels and warmer temperatures favor fungal colonization. Heating, Ventilation, and Air Conditioning Humidity control systems (HVAC) units maintain humidity levels and temperatures to decrease fungal activity [202].

Water accumulation is a critical factor for fungal growth and moment colonization by fungal species [217]. Therefore, is important to implement effective drainage systems, such as gutters and downspouts, to prevent moisture accumulation by redirecting water away from the monument's foundation and surfaces [218]. Other measures include proper landscaping and grading to minimize water pooling [218,220], using porous materials to allow rainwater to penetrate the ground, and applying waterproof and moisture-resistant coatings to monuments to prevent groundwater intrusion [221]. Cleofas and co-workers demonstrated [222] the prevalence of fungal growth in five flood-prone public elementary schools. The frequency of flood occurrence was associated with the

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prevalence of fungi in the study sites. Among the materials inside the classrooms, the students' chairs harbored the greatest number of visible fungal growth primarily because they are made up of wood [222].

6.2. Cleaning and Removal:

Several techniques have been developed to control cultural heritage microbial deterioration, including chemical, physical, and biological methods.

Chemical treatments, such as biocides and fungicides, inhibit fungal colonization and disrupt the life cycle of the organisms responsible for the biodeterioration. However, the use of these products requires careful consideration, meaning that the appropriate fungicide must be selected to be effective against the specific fungi while minimizing harm to the monument and the environment [223,224]. In recent years, innovative materials and techniques have emerged to protect these monuments and artifacts. Nanoparticles (hydroxide, silver, copper, and zinc oxide), incorporated into protective coatings, paints, or other materials, penetrate fungal cell walls, disrupt cellular processes and inhibit growth, and constitute a cutting-edge solution for preserving monuments affected by fungal degradation [225,226]. Other alternatives are microemulsions. These colloidal dispersions of water, oil, and surfactants constitute a platform for delivering various active ingredients, such as fungicides and consolidants, to the monument surface. Micelles, self-assembling structures formed by surfactant molecules in a solution, encapsulate and solubilize hydrophobic compounds, such as fungicides, enhancing their bioavailability. Functional gels are thixotropic materials loaded with active agents, such as fungicides and consolidants, that adhere to vertical surfaces, and allow the agent to have a long-lasting effect [227,228].

Physical methods, such as mechanical fungal removal, include gentle methods like brushing and vacuuming. These methods suit lightly contaminated areas and physically remove fungal growth without damaging the monument. Ultra-violet radiation, especially UV-C, damages fungal DNA and effectively reduces fungal colonization without chemical residues [229]. Gamma radiation disrupts cellular processes, preventing fungal growth. Highly effective at eliminating fungal colonization, it poses minimal risk to the structural integrity of monuments and artifacts [230]. Laser cleaning utilizes targeted laser technology to selectively remove fungal growth from surfaces without damaging the underlying material [231,232]. Heat shock involves subjecting surfaces with fungi to controlled temperature increases that disrupt fungal cell membranes and inhibit their growth [233]. On the contrary, cryogenic cleaning uses dry ice pellets accelerated by compressed air to remove fungal growth [234]. Both techniques are non-abrasive, leave no residue, and are environmentally friendly [233,234]. Finally, microwaves generate electromagnetic radiation that heats fungal cells, disrupting their cellular structure and inhibiting growth, removing fungal biofilms and contaminants [230,235].

Biological methods harness the power of natural molecules with biocidal activity, enzymes, and microorganisms to limit fungal colonization and ensure the longevity of monuments effectively. Natural molecules often possess inherent biocidal properties, acting as natural fungicides. Among these molecules are essential oils (e.g., tea tree oil, thyme oil, and oregano oil), tannins, and copper-based compounds (e.g., copper sulfate) [236,237]. These molecules are biodegradable, non-toxic, and environmentally friendly, safely applied without harming the monument or the surrounding ecosystem [238]. Enzymes (e.g., cellulases and proteases) are biological catalysts that degrade organic matter. These treatments are used under controlled conditions to ensure the enzymes target fungal contamination and preserve the monument [239]. Certain microorganisms (e.g., *Streptomyces* spp. and *Trichoderma* spp.) outcompete or antagonize pathogenic fungi and establish a natural balance that discourages fungal colonization when applied to monument surfaces or the surrounding environment [240,241].

6.3. Consolidation and Reinforcement:

Over time, fungal colonization compromises monument stability, making it necessary to implement consolidation and reinforcement strategies.

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Consolidation involves strengthening and stabilizing deteriorated surfaces, particularly porous materials (e.g., stone, wood, or plaster), to restore cohesion and structural integrity. Consolidation helps prevent further fragmentation or detachment of surfaces affected by fungal degradation. Treated surfaces become more resistant to environmental factors, reducing the risk of further deterioration. Finally, this technique improves the monument's appearance by restoring lost details and texture [242].

Reinforcement, which involves adding supplementary materials (e.g., steel rods, fiberglass, or carbon fiber composites) or structural repairs (e.g., reconstruction or repair work) to enhance monument structural stability, is particularly relevant when fungal degradation has deeply compromised its load-bearing capacity. These measures strengthen the monument's overall structure by mitigating the risk of collapse or further damage, extending the monument's lifespan, ensuring its preservation for future generations, and enhancing safety, reducing the risk of accidents caused by unstable monument structures [243].

6.4. Surface Treatments:

Surface treatments are essential to preserving monuments and artifacts. These treatments include applying different types of coatings (i.e., protective - contains fungicides and creates a physical barrier on monument surfaces, consolidating - protects and consolidates deteriorated surfaces, and barrier coatings - repels water) that provide fungal and weather resistance and enhance durability [244,245].

Sealants (flexible or consolidating) are applied to fill cracks, gaps, and voids in monument surfaces, preventing moisture infiltration and fungal colonization. These products ensure waterproofing, structural protection, and appearance enhancement [246].

6.5. Replication and Replacement:

In some cases, replication and replacement become necessary strategies to ensure the longevity of monuments and the retention of their historical and cultural significance.

Replication of decorative elements involves the creation of accurate reproductions of damaged or missing pieces using traditional techniques, materials, and craftsmanship. This technique assures historical authenticity since the replicated parts closely resemble the original ones, aesthetic restoration by reinstating missing or deteriorated features, structural integrity once reproduced elements reinforce structural stability when used with authentic materials, and replacement of damaged sections with matching materials to maintain the monument's integrity [247].

Replacement involves removing and replacing entire sections or components that are so damaged that they cannot be restored. New materials are carefully selected to match the original aesthetics. This technique assures structural integrity, aesthetic continuity, and monument preservation [248].

6.6. Monitoring:

Monitoring is fundamental for conservation efforts, ensuring that monuments remain structurally sound, aesthetically pleasing, and protected against the forces of time and nature.

Regular visual inspections are critical in monument monitoring to detect signs of fungal colonization, structural damage, or deterioration. These inspections should be conducted by trained conservators or professionals familiar with monument preservation [249]. Traditionally, fungal spore monitorization can be performed using viable volumetric sampling methods [250–253]. However, modern technology (e.g., remote sensing, digital imaging, and Infra-red thermography) are used to assess the condition of monuments and detect hidden damage or areas of concern not visible to the naked eye [254–256]. Environmental conditions (e.g., temperature, relative humidity, and pollution levels) cause harmful effects on the cultural heritage assets, being critical to implement effective and reliable monitoring systems to continuously assess environmental conditions and determine the need for some specific action for heritage safeguard [257]. Likewise, fungal analysis on surfaces and

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circulating air is required to identify specific fungal species present. Traditional include culture-based methods using a variety of standardized media, such as MEA, DG18, and dichlorane rose Bengal (DRBC) medium. The advent of molecular techniques, including molecular markers such as the Internal Transcribed Spacers (ITS regions), provides a deeper understanding of these fungal communities [258]. More recently, next-generation sequencing techniques have been used for this purpose, reviling an even greater diversity of communities when compared to the Sanger method and allowing to study the interrelationships between different microorganisms [259]. This information helps conservators effectively tailor treatment strategies to target the predominant fungal threats.

6.7. Documentation and Research:

When fungal degradation threatens monuments and artifacts, comprehensive documentation and research are indispensable to understand, conserve, and safeguard cultural heritage.

Documentation of the monument must include historical records that serve as reference materials for restoration and replication efforts, detailed condition assessments document of the current state of monuments to track changes over time, materials analysis to select the appropriate conservation treatments, fungal analysis to determine treatment strategies and assess the potential for further damage, and treatment records of any changes made to the monument's structure or appearance [260].

Research must focus on fungal ecology that informs on preventive measures and treatment strategies, treatment developments including the testing of new consolidants, biocides, and surface treatments, historical context that informs on decisions regarding replication, replacement, and restoration to ensure authenticity, environmental impact assessing the ecological consequences of treatments and ensuring they align with sustainability goals, preventive measures including studies on drainage systems, vegetation management, and visitor impact, public awareness promoting a sense of ownership and responsibility among communities and visitors toward monument preservation, and technological advancements that aid in documentation, assessment, and research efforts [261].

7. Conclusions

This work delves into the intricate relationship between fungal diversity and heritage degradation, exploring various facets of this complex issue. Firstly, the diverse range of monuments were described, recognizing that the heterogeneity of these structures tailors all preservation strategies. Secondly, materials that constitute these monuments were presented, emphasizing the susceptibility of these materials to fungal degradation. Understanding the vulnerabilities of these materials is paramount for adequate preservation. Thirdly, the multifaceted factors influencing fungal colonization and proliferation were discussed (e.g., moisture levels, temperature, and pollution), acknowledging that these factors empower conservators to implement preventive measures and targeted treatments. Lastly, various preservation and restoration techniques were explored, from biocidal treatments to consolidation methods, offering solutions that balance efficacy with preserving historical and aesthetic authenticity. Preserving cultural heritage is a multifaceted endeavor that requires a deep understanding of fungal diversity, monument materials, environmental factors, and conservation techniques. Ensuring that the heritage endures for future generations is crucial and mitigating the destructive impact of fungal degradation is paramount.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org. **Figure S1**: Ukraine's heritage destroyed during the Russian invasion of Ukraine (https://www.unesco.org/en/articles/damaged-cultural-sites-ukraine-verified-unesco), distributed by the different Oblasts (A) and heritage type (B).; **Table S1**: Cultural heritage and the materials used for its construction, including its characteristics, applications, examples, and fungi associated with its degradation (the most common fungi are presented in bold).

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