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Potential Application of Melanins for Restoring War-affected Soils in Ukraine

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The extensive environmental degradation of terrestrial ecosystems, particularly agricultural soils, in Ukraine following the Russian full-scale invasion necessitates the rapid development of innovative and scalable remediation strategies. Conventional soil restoration methodologies are frequently constrained by factors such as cost, labor intensity, and limited applicability across the vast and complex areas afflicted by military activities. This manuscript presents a comprehensive synthesis of current knowledge regarding melanin, a ubiquitous biopolymer, positing its substantial potential as a sustainable and efficacious soil amendment for the rehabilitation of war-affected landscapes. Melanin's diverse biogenic origins in soil, predominantly from microbial biosynthesis pathways, alongside its accumulation from decomposed organic matter, underscore its widespread natural availability. We elucidate its critical properties and ecological functions, including its exceptional capacity for heavy metal and radionuclide sequestration through complexation with its abundant phenolic and carboxylic groups. Furthermore, melanin's contribution to long-term soil organic matter stabilization, its potent antioxidant and UV-shielding capabilities, and its role in modulating beneficial microorganism-plant interactions are critically discussed, highlighting its multifaceted contribution to soil health and resilience. The inherent attributes of melanin inform its potential applications in soil remediation, ranging from the direct application of melanogenic microorganisms for contaminant immobilization and enhanced revegetation to the development of engineered melanin-based materials for targeted pollutant removal. While acknowledging the significant promise, challenges such as optimizing its in-situ mobility, ensuring scalable and cost-effective production, and comprehensively assessing long-term ecological impacts remain pertinent research avenues. Future research should focus on the synergistic integration of melanin with complementary soil amendments, particularly silicon-based compounds, which can provide additional benefits in terms of structural stability and plant stress tolerance, thereby fostering a holistic approach to post-conflict ecological restoration.

Keywords: melanin, melanin-producing microorganisms, soil remediation, war-affected soils

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Introduction

The full-scale invasion launched by Russia on February 24, 2022, has had a devastating impact on terrestrial ecosystems, particularly the soils of Ukraine (Didenko, 2024). Approximately 30% of the country will require surveying and humanitarian demining (Osmolovska and Bilyk, 2024). However, even after demining, soils marked by bomb craters, destroyed military equipment, oil spills, fire damage, and landslides may continue to pose significant environmental risks and limit agricultural productivity (Koshel et al., 2024). The structural alterations of soils caused by explosions are relatively easy to detect and characterize. These include destruction, redistribution, and compaction of soil layers; such soils are classified as bombturbated (Hupy & Schaetzl, 2006). Far less is known about changes in the chemical and biological properties of war-affected soils, particularly regarding soil organic matter and contamination of toxic substances.

In a global context, Barakat and Zyck (2009) and Certini et al. (2013) report comparable consequences in conflict-affected regions of the Middle East and Italy, including soil degradation, reduced water-holding capacity, erosion, and the loss of microbial diversity. Consequently, the Ukrainian experience and the tools developed may offer valuable insights for application in Syria, Lebanon, Iraq, and other post-conflict regions.

A threat to food security both within Ukraine and beyond its borders has emerged due to the decline in agricultural land productivity in one of the world's key grain-exporting countries. Effective strategies for restoring war-affected soils have yet to be developed. Given the scale of the problem – thousands of square kilometers require rehabilitation – the use of conventional soil restoration methods is limited due to a number of reasons like cost, labor intensity, suitability for large-scale application, and potential for further disturbance. A comprehensive policy should be proposed to manage the agrophysical, agrochemical, and biological properties of soils contaminated as a result of military activities. This policy should aim to minimise the environmental impact of the war, restore soil fertility, and create conditions for sustainable land use.

One promising approach to large-scale soil rehabilitation in Ukraine involves the use of soil amendments. Unlike conventional fertilizers, which are applied in larger amounts primarily for nutrient supply, soil amendments are typically used in smaller quantities to enhance soil structure, chemistry, and biology. Among these, melanin, a naturally occurring biopolymer, has emerged as a particularly promising candidate for remediation efforts due to its high stability, strong chelating and sorption capacities, antioxidant properties, and protective effects against environmental stressors.

This study synthesizes current knowledge on the role of melanin in soil systems, with a focus on its potential application in the restoration of war-affected soils in Ukraine. By examining its functional properties, we aim to contribute to the development of scalable and sustainable strategies for post-conflict ecological rehabilitation.

Sources of Melanin in Soils

The most common sources of melanin in soil are bacteria and fungi. Soil microorganisms, including bacteria, actinomycetes, and fungi, serve as the primary biogenic producers of melanin, which plays protective, structural, and adaptive roles in microbial cells. Microbially synthesised melanin is characterised by high stability, strong chelating capacity, and notable antioxidant activity, making it a valuable component of soil ecosystems (Singh et al., 2021).

The biosynthesis of microbial melanin primarily proceeds via two major pathways: the L-3,4-dihydroxyphenylalanine (L-DOPA) pathway and the 1,8-dihydroxynaphthalene (DHN). These ways are mediated by enzymes such as tyrosinase, laccase, and polyketide synthase (Singh et al., 2021; Dalfard et al., 2006). It is noteworthy that certain microbial strains can utilise multiple precursors and enzymatic pathways simultaneously, complicating the structural characterisation of the resulting melanin (Singh et al., 2021).

The genus *Streptomyces* is an important group of melanin producers in soil environments. For example, the strain *Streptomyces glaucescens* NEAE-H, isolated from Egyptian soils, produced up to 31.650 µg of melanin per 0.1 ml of medium, with tyrosinase activity reaching 6,089 $U.ml^{-1}$. Optimisation of cultivation conditions, including a 6-day incubation period, the presence of proteose peptone, and ferric ammonium citrate, significantly enhanced pigment yield (El-Naggar et al., 2017). Comparable results have been obtained for other *Streptomyces* isolates, including strains that produce melanin with high thermostability and resistance to organic solvents (Dalfard et al., 2006). Furthermore, El-Batal et al. (2016) report the stimulation of melanin production in *Streptomyces cyaneus* via gamma irradiation, followed by the application of the pigment in the synthesis of copper oxide nanoparticles.

Actinomycetes, particularly those isolated from complex environments such as petrochemically contaminated soils, have demonstrated the ability to synthesise extracellular melanin, which provides resistance to toxic metals and oxidative stress (Castro-Sowinski, 2002; Amal et al., 2011; Singh et al., 2021). Studies indicate that only 5–10% of actinomycete strains are capable of melanogenesis. However, these strains can produce melanin in high concentrations (El-Batal et al., 2016).

Bacteria of the genus *Bacillus* also exhibit considerable potential. For example, *Bacillus safensis* was able to produce melanin using a fruit-based medium, reducing production costs. The resulting pigment exhibited UV-protective, chelating, and antioxidant properties. Another isolate, *Bacillus thuringiensis*, synthesised melanin from tyrosine and demonstrated resistance to hydrogen (H_2O_2), suggesting its adaptive capacity under stress conditions (Singh et al., 2021). Although references to melanin production by *Bacillus* sp. are relatively limited, their ability to synthesise melanin via oxidative mechanisms is considered well-established (Nosanchuk et al., 2003).

Fungi are known to be capable of synthesizing several types of melanin, which depend on their metabolic characteristics and environmental conditions. Most fungal melanins are classified as allomelanins, which are characterised by their lack of nitrogen, differentiating them from other types of melanin, such as DOPA-melanin found in animals. Among allomelanins, DHN-melanin is identified as the most common, synthesized through the polymerization of 1,8-dihydroxynaphthalene (DHN) (Mattoon et al., 2021).

Melanin particles derived from fungal or bacterial sources have been shown to form stable complexes with metal ions, even in the presence of competing ions (Fogarty & Tobin, 1996; Garcia-Rivera and Casadevall, 2001). This is supported by the fact that extracellular melanin from *Cryptococcus neoformans* was found to bind silver ions and protect cells from the toxic effects of $AgNO_3$ (Garcia-Rivera and Casadevall, 2001).

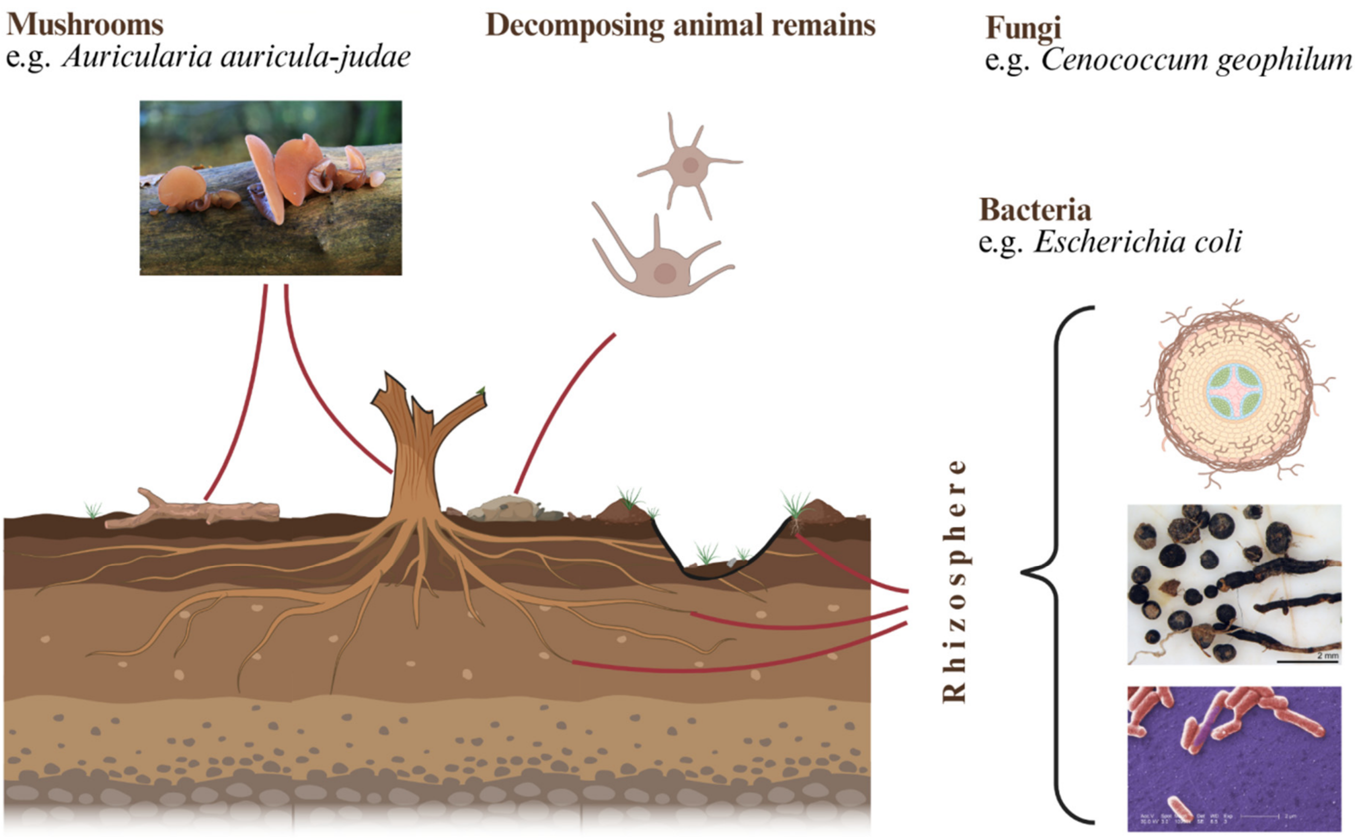

Figure 1 Main sources of melanin in war-affected soils
Image credits: *Auricularia auricula-judae* by Stu's Images, CC BY-SA 4.0; *Cenococcum geophilum* by Jerry Cooper, CC BY 4.0; *Escherichia coli* courtesy of CDC/Janice Haney Carr
Source: Figure created with BioRender.com

While microscopic fungi and bacteria are the most important producers of melanin, in war-affected landscapes there are several other significant sources of melanin-like substances (Figure 1). On a local scale, input of melanin from several widely-abundant species of mushroom-forming fungi, e.g. *Auricularia auricula-judae* (Agaricomycetes) may be significant (Ma et al., 2018), because they colonise damaged trees and large woody debris in high numbers.

In war-related contexts, a significant source of melanins is human and animal corpses. Dead bodies contain melanin in skin, hair, eyes, and nervous tissue (Lerner et al., 1950). This melanin not only persists after death but also affects the microbial breakdown of other organic materials due to antioxidant (Borges et al., 2001) and metal chelating (Saiz-Jimenez, 1995; Wilson et al., 2007) properties.

For instance, research on hair from archaeological and forensic contexts has shown that melanin is still detectable even when complete keratin degradation has occurred (Wilson et al., 2007). This longevity is due to the complex cross-linked structure of eumelanin, which resists typical enzymatic degradation by decomposer microorganisms. Therefore, melanin from corpses acts as a durable component in humus formation, like stable carbon forms like black carbon (Saiz-Jimenez, 1995).

In addition to their direct input, organic residues also stimulate secondary melanogenesis in microorganisms (Borges et al., 2001). Detritivorous fungi, particularly species from the genus *Cladosporium*, *Alternaria*, produce melanin intensively in response to protein-rich substrates, including remnants of muscle and connective tissues (Scheu et al., 2004).

Ionizing radiation, characteristic of conflict zones or contaminated areas, enhances melanogenic activity in melanised filamentous fungi. Studies in the Chornobyl Exclusion Zone have shown that darkly pigmented fungal species, such as *Cladosporium* and *Alternaria*, tend to dominate radioactive soils. This is interpreted as both a protective mechanism and a means of immobilizing toxic metal via melanin deposition in cell walls (Zhdanova et al., 2004).

Consequently, corpse decomposition generates distinct ecotopes enriched in stable organic compounds. In this context, melanin acts as a dual agent, both as a persistent biomolecule and as an induced microbial metabolite. This process is critical to the formation of structural humus, particularly in high-intensity biodegradation hotspots such as mass graves, faunal decomposition sites, or areas of human mortality resulting from armed conflict.

Environmental Functions and Key Properties of Melanin in Soil Ecosystem

Melanin, due to its complex polymeric structure, exhibits an exceptional capacity for the sorption of a wide range of heavy metals and radionuclides. Its chemical reactivity is attributed to the presence of numerous functional groups (phenolic, carboxylic, quinonoid, and amino groups) that are capable of coordinating metal ions to form both weak surface interactions and stable inner-sphere complexes (Senesi et al., 1987; Fogarty et al., 1996; Costa et al., 2012).

In soil environments, melanin exhibits functional similarities to humic acid in its role as an active organic colloid with a high capacity for metal complexation. According to (Senesi et al., 1987), melanins synthesized by soil fungi (such as *Aspergillus glaucus*, *Eurotium echinulatum*, and *Hendersonula toruloidea*) contain both water-soluble and acid-resistant binding sites for Cu(II) and Fe(III). The overall sorption capacity was found to correlate positively with nitrogen content and polymer acidity. Spectroscopic analyses confirmed the formation of coordination bonds involving carboxylic and phenolic groups.

Melanin biosynthesis in fungi such as *Cryptococcus neoformans*, *Aspergillus* spp., and *Cladosporium* is mediated by enzymes such as laccase and tyrosinase, which facilitate the cell's defensive response, particularly during interactions with plant metabolites or pathogens (Drewnowska et al., 2015; Singh et al., 2021). Moreover, the enzyme laccase, which participates in melanin biosynthesis, has been identified in various soil bacteria, particularly among rhizospheric species. This suggests that melanogenesis may be a common trait in microbial communities of the root zone (Singh et al., 2021).

Other studies have demonstrated that both natural and synthetic forms of melanin (e.g., eumelanin derived from tyrosine) effectively bind toxic metal ions such as Pb(II), Cu(II), Cr(VI), Zn(II), and U(VI), exhibiting high sorption capacities – up to 167.8 $mg.g^{-1}$ for Cu(II) (Manirethan et al., 2018). The ability of melanin to chelate metal ions has also been confirmed by electron spin resonance (ESR) and infrared (IR) spectroscopy, both of which detect spectral shifts upon saturation with Cu(II) or Fe(III) (Costa et al., 2012; Senesi et al., 1987). The resulting complexes remain stable across a wide pH range, a critical feature for applications in variable environmental conditions (Costa et al., 2012).

Recent studies have focused on melanin extracted from marine sources (Manirethan et al., 2018) confirming its high selectivity and stability in binding Pb(II), Hg(II), and Cr(VI), which is particularly relevant for the remediation of environments affected by military operations or industrial pollution. Additionally, according to (Fogarty et al., 1996; Chatelain et al., 2014), melanin can participate in the sequestration of radionuclides, thereby reducing their bioavailability.

One of the key properties of microbial melanin is its resistance to chemical degradation and high sorption capacity, both of which are directly linked to its interactions with soil components, particularly mineral and organic matter. The solubility and retention of melanin are influenced by the physicochemical characteristics of the soil, including mineral composition, organic matter content, pH, and ionic composition.

Soil types rich in aluminosilicate clays, especially montmorillonite and kaolinite, significantly affect the structure and stability of melanin. Kadoshnikov et al. (1999) demonstrated that melanin produced by the microfungus *Cladosporium cladosporioides* forms stable associations with clay minerals through hydrogen bonding, coordination complex formation, and ligand exchange between the carboxyl groups of melanin and exchangeable cations on mineral surfaces. These interactions enhance melanin retention in the soil matrix and contribute to its long-term persistence, particularly in zones at risk of chemical contamination.

Moreover, the structural similarity between melanin and humic acids has been confirmed in studies such as (Schnitzer and Chan, 1986), which compared the properties of fungal melanin and soil-derived humic substances. It was found that melanin contains a higher proportion of phenolic compounds, exhibits stronger acidity, and retains aliphatic chains after hydrolysis, making it less biodegradable than humic acids. This indicates that melanin can persist for longer periods in soils with low mineralization and high organic matter content.

Under most soil conditions, melanin is characterized by extremely low solubility due to its hydrophobic nature and high molecular weight. However, Munoz-Torres et al. (2024) noted that under strongly alkaline pH or in the presence of strong bases (e.g., NaOH), melanin can undergo fragmentation and partial solubilization, which affects its bioavailability. At the same time, such treatment alters its chemical structure, reducing its natural protective properties, particularly its capacity to chelate heavy metals.

Melanin, as a biopolymer with pronounced chelating and antioxidant properties, exhibits a high affinity for mineral surfaces, particularly clay minerals and soil organic matter. These interactions affect melanin's biostability, its susceptibility to microbial degradation, and its ability to form long-lasting associations within the soil environment.

Fomina and Gadd (2002) demonstrated that in the presence of clay minerals, specifically bentonite, kaolinite, and palygorskite, melanin-producing fungi (*Cladosporium cladosporioides*, *C. herbarum*, *Humicola grisea*) form more compact and structurally complex pellets. The microstructure of these pellets displays a zonal organization: a central core composed of a clay-mycelium composite, a middle layer with dispersed mycelium and clay particles, and an outer "fibrous" layer. This structure indicates the physical incorporation of clay into the fungal biomass, potentially stabilizing both the melanin itself and the metal-binding capacity of the fungal cells.

Further studies by the same research group have shown that combining clay, particularly bentonite, with melanin-containing fungal biomass significantly enhances the sorption capacity for heavy metals compared to the individual components. Bentonite contributes not only to increased sorption capacity but also to the formation of new functional surfaces at the biomineral interface (Fomina and Gadd, 2002).

Other studies confirm that clay minerals function not only as matrices for melanin retention but also as active participants in its stabilization through cation exchange, hydrogen bonding, and the sorption of functional groups. In particular, iron oxides and aluminosilicates such as vermiculite and illite exhibit high affinity for the carboxyl and phenolic groups of melanin and soil organic matter in general. According to Chen et al. (2014), close spatial associations between carbon and Fe-, Al-, and Si-bearing minerals were identified in soil particles, indicating the stable incorporation of melanoid and humic fractions into the structure of organo-mineral complexes.

Burford et al. (2003) further highlight the role of fungi in mineral bioweathering, particularly in the formation of secondary mycogenic minerals. Through the activity of their metabolites, especially melanin, fungi can

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exert oxidative effects on minerals (e.g., silicates and carbonates), promoting metal mobilization and the development of stable organo-mineral structures.

Moreover, as shown by Lenaers et al. (2018), melanin significantly contributes to the hydrophobicity of fungal biomass and its resistance to mineralization, which is essential for the long-term accumulation of organic matter in soils, particularly in acidic or podzolic environments.

Overall, the presence of clay minerals and organic matter in the soil creates optimal conditions for the binding, stabilization, and prolonged functionality of melanin. Its interaction with clay materials not only enhances the biological stability of the pigment but also considerably expands its ecological functions.

Melanin polymers in soil play a pivotal role in the long-term stabilization of organic matter, primarily due to their high chemical resistance and hydrophobicity, which make them resilient to microbial degradation (Bloomfield and Alexander, 1967). Melanin exhibits a complex polyaromatic structure, similar to that of humic substances, allowing it to bind with proteins, polysaccharides, and lignins to form stable organo-mineral complexes (Knicker et al., 1995; Sun et al., 2021).

In addition, melanin can retard the decomposition of organic carbon by inhibiting the enzymatic activity of microorganisms involved in humus degradation. For example, Roy and Rhim (2021) demonstrated that melanin-producing fungi suppress the activity of hydrolytic enzymes, such as cellulase and lipase, thereby indirectly delaying the mineralization of organic matter.

Melanin can also impede oxygen diffusion to organic substrates by forming a hydrophobic barrier, thereby decreasing the rate of aerobic decomposition of humic fractions (Sun et al., 2021). This effect is especially pronounced in lignin-rich soils, where melanin interacts with phenolic compounds to form insoluble, condensed complexes that are highly resistant to mineralization (Knicker et al., 1995; Treseder and Lennon, 2015).

An additional key stabilization mechanism involves the physical immobilization of carbon through melanin-clay mineral interactions. As reported by Knicker et al. (1995) and Malik and Haider (1982), melanin can function as a molecular bridge between mineral particles and humic acids, facilitating the formation of microaggregates that are resistant to biodegradation.

Bloomfield and Alexander (1967) reported that fungal melanin components can increase cellular resistance to lysis and autolysis, thereby limiting the release of soluble organic compounds into the microbial pool, constituting an additional mechanism for delaying decomposition.

Sun et al. (2021) also demonstrated that melanin-producing fungi, particularly in association with lignin-rich substrates, promote the accumulation of stable carbon in soils, which may serve as an important tool for long-term carbon sequestration.

Thus, melanin acts as a key natural stabilizer of humus, operating through its chemical inertness, sorptive capacity (Malik & Haider, 1982), anti-enzymatic activity (Knicker et al., 1995), and its role in the formation of stable aggregates in the soil matrix (Fernandez and Koide, 2014).

Melanin serves not only as a protective pigment but also as a key modulator of interactions between microorganisms and plants, particularly within the soil environment. Its presence within microbial communities can significantly affect community structural stability, nutrient bioavailability (Rangel et al., 2018), and resilience to environmental stressors (Singh et al., 2021).

Melanin-producing microorganisms exhibit enhanced colonisation of the rhizosphere, a trait linked to the pigment's ability to protect cells from ultraviolet radiation, oxidative stress, temperature fluctuations, and nutrient limitations (Nosanchuk et al., 2003; Rangel et al., 2018; Wang et al., 2020). For example, *Vibrio natriegens* genetically modified to synthesise melanin displays increased tolerance to hydrogen peroxide, underscoring melanin's antioxidant properties and its potential in the development of stress-resistant bioagents (Wang et al., 2020).

In melanin-producing fungal biocontrol agents, such as *Trichoderma* spp., melanin plays a dual role, protecting fungal cells from environmental stress and enhancing ecological competitiveness through the synthesis of secondary metabolites (Singh et al., 2021). They also highlighted the role of fungal melanin in promoting plant–microbe interactions and microbial fitness in the soil environment.

Castro-Sowinski (2002) showed that co-inoculation with melanin-producing strains of *Sinorhizobium meliloti* and *Azospirillum brasilense* significantly improved rice growth, both in terms of biomass and yield. These findings support the role of melanin in stimulating phytohormonal regulation and enhancing biological nitrogen fixation.

Furthermore, Nosanchuk et al. (2003) reported that melanin enhances the ability of microbial cells to form biofilm-structured communities that improve microbial survival under environmental stress and may facilitate stable colonisation in soil environments.

Beyond its direct protective role, melanin also influences the structure of soil ecosystems. It stabilizes microbial communities, enhances their activity in carbon and nitrogen transformation processes, and promotes the development of metabolically active populations during the degradation of organic residues (Rangel et al., 2018; Singh et al., 2021).

Accordingly, melanin functions as a key mediator in the microorganism-plant-soil system, simultaneously increasing stress tolerance (Wang et al., 2020; Singh et al., 2021), facilitating more efficient nutrient uptake, and improving the overall biofunctionality of agroecosystems.

Melanin is an essential ecological function in soil environments by acting as a natural barrier to ultraviolet (UV) radiation, shielding microorganisms from DNA photodamage and structural cellular injury. Its capacity to absorb a wide UV spectrum and dissipate the energy as heat effectively mitigates photostress, thereby promoting microbial survival under extreme environmental conditions (Ragon et al., 2011; Kunwar et al., 2012; Cao et al., 2021). Microbial communities colonizing exposed surfaces, such as sandy soils, rock, or minimally vegetated terrains, commonly synthesize melanin as an adaptive response to high solar irradiance (Ragon et al., 2011).

In addition to UV shielding, melanin functions as a robust antioxidant, capable of neutralising various reactive oxygen species (ROS) such as superoxide anions, hydroxyl radicals, and peroxides. Its polyphenolic architecture and high redox potential allow it to act as an efficient free radical scavenger, thereby preventing oxidative damage to cellular macromolecules, including proteins, lipids, and nucleic acids (Pombeiro-Sponchiado et al., 2017; Cao et al., 2021; Singh et al., 2021). Experimental studies using model microorganisms have demonstrated that melanin improves cellular resilience to oxidative stress, attenuating apoptosis and preserving metabolic activity even under oxidative challenges such as hydrogen peroxide (H_2O_2) or γ-radiation exposure (Pombeiro-Sponchiado et al., 2017; Cao et al., 2021).

The protective role of melanin is substantiated by findings from extreme ecosystems such as Arctic and Antarctic environments, and even orbital flight conditions. The melanized fungus *Cryomyces antarcticus* exhibits remarkable resistance to UV-B and cosmic radiation, underscoring the potential application of melanin as a bioprotective layer for microorganisms in extraterrestrial and other high-stress habitats (Pacelli et al., 2017).

Within soil environments, melanin contributes to the long-term resilience of microbial communities by forming a semi-permeable barrier against exogenous oxidants. Studies on mycorrhizal fungi have demonstrated that melanin limits the diffusion of ROS into fungal cells and suppresses enzymatic oxidation, especially under conditions of thermal or chemical stress (Fernandez and Koide, 2014).

Melanin also functions as a cell wall modulator in fungi and bacteria, decreasing permeability and enhancing cellular resistance to radiation, antibiotics, and heavy metals. This has been evidenced in studies by (Nosanchuk and Casadevall, 2003), where melanin-producing microorganisms displayed increased resistance to antimicrobial agents and a lower mutation rate.

Melanin has also been proposed as a component of bioengineered protective coatings and bioactive soil amendments. For example, Ragon et al. (2011) investigated melanin-based biofilms as shielding materials for microorganisms in the regolith, with potential applications in Martian (Pacelli et al., 2017) and arid terrestrial soils (Singh et al., 2021).

Melanin synthesis by microorganisms is a complex process that is highly sensitive to environmental conditions, such as temperature, humidity, and pH fluctuations. In soil ecosystems, these factors play a critical role in microbial survival and in the intensity of melanogenesis, which serves as an adaptive mechanism under stress conditions.

Temperature is one of the primary factors regulating melanin biosynthesis, particularly in soil-dwelling fungi and bacteria. According to Eisenman and Casadevall (2011), melanized fungi exhibit enhanced survival under stressors such as ultraviolet and ionizing radiation, as well as thermal extremes. This resilience is attributed to melanin's ability to stabilize cellular structures, especially through its accumulation in the cell wall (Eisenman and Casadevall, 2011).

The enzymatic activity responsible for melanin synthesis is strongly temperature-dependent. For example, Singh et al. (2021) report that fermentation at optimal temperatures leads to increased microbial biomass, which in turn correlates with a higher melanin yield.

El-Bialy et al. (2019) found that exposure to terbinafine, an antifungal agent that induces cellular stress, led to a significant increase in both intracellular and extracellular melanin production in the yeast, like form of *Aureobasidium pullulans*. Although the study did not focus specifically on temperature, it was conducted under controlled conditions (30 °C), suggesting that this temperature is favorable for melanogenesis. Moisture availability also affects the intensity of melanin production. Melanin plays a protective role under desiccating conditions by reducing water loss from the cell. They also showed that under high salinity stress, the survival rate of melanized cells was higher than that of non-melanized cells, and pigment production was significantly enhanced. These findings highlight the functional role of melanin in regulating osmotic pressure and stabilizing the cell membrane under water-limiting conditions.

The acidity of the environment (pH) indirectly affects the activity of key enzymes involved in melanin synthesis, such as tyrosinase and laccase. Singh et al. (2021) reported the optimal pH values for microbial melanogenesis vary depending on the microbial species. In most bacteria, melanin production is more efficient under neutral to slightly alkaline conditions, whereas certain fungi exhibit enhanced melanin synthesis in more acidic environments. Eisenman and Casadevall (2011) noted that fungal melanin is typically localized in the cell wall and may be formed via vesicular transport, with its biochemical functionality partially influenced by the external pH of the environment.

Therefore, melanin synthesis is generally upregulated under stress conditions, including temperature fluctuations, osmotic imbalances, and changes in pH. These environmental factors either directly affect the enzymatic activity of melanin biosynthesis or trigger melanin production as an adaptive response by microorganisms to unfavorable conditions.

Applications of Melanin in Soil Remediation

The use of melanin-producing microorganisms in military conflict zones represents a novel and promising approach to bioremediation. Soils in areas of active warfare are typically characterized by elevated concentrations of heavy metals, radionuclides, and residues of explosive compounds, creating highly challenging conditions for ecosystem restoration.

Studies conducted in radiation-contaminated environments, such as the Chornobyl Exclusion Zone (Pombeiro-Sponchiado et al., 2017), have shown that micromycetes, particularly *Cladosporium cladosporioides* and other melanized fungi, actively colonize radioactive substrates. These fungi not only survive but also exhibit a remarkable adaptive tolerance to ionizing radiation, attributed to the high melanin content in their cell walls. Melanin acts as a biological shield, absorbing both β- and γ-radiation and protecting intracellular structures. Notably, the uptake of radiocesium-137 and radiocobalt-60 by melanized fungi was greater than that of nonmelanized strains.

These studies also confirm the effectiveness of melanin in binding heavy metal ions. For example, the biomass of *Aspergillus nidulans* with elevated melanin production exhibited up to 75% higher sorption of neodymium and lanthanum compared to control cultures, underscoring the role of pigmentation in bioaccumulation processes. In another study, melanized rhizomorphs of *Armillaria* were found to accumulate metals (Al, Zn, Fe, Cu, Pb) at concentrations 50 to 100 times higher than those present in the surrounding soil (Pombeiro-Sponchiado et al., 2017).

According to Fogarty et al. (1996), melanized fungal strains exhibit 2.5-6 times higher metal sorption capacity than their albino counterparts. Fomina and Gadd (2002), showed that culturing fungi on media supplemented with bentonite not only enhances melanin stability but also preserves or even improves its sorptive efficiency. These findings highlight the potential for developing bio-mineral sorbents for environmental remediation of polluted sites.

Additional examples involve bacteria such as *Azotobacter chroococcum*, which are capable of synthesizing melanin under stress conditions, particularly in the presence of cadmium, chromium, and nickel. These organisms not only fix atmospheric nitrogen but also protect plants in environments with elevated levels of toxicants, making them especially valuable for supporting vegetation reintegration in war-degraded landscapes (Singh et al., 2021).

Under field conditions, melanin can be applied in the form of nanostructured particles or filters. For example, Manirethan et al. (2018) demonstrated that coating melanin onto carriers (e.g., activated carbon) enables the development of efficient sorption systems for the removal of chromium, lead, copper, and mercury from water, even at low concentrations, meeting WHO standards for drinking water quality.

In microbial communities developing in soils of various types, the interaction between melanin and clay minerals also has biotic implications. For example, the formation of biomineral sorbents based on fungal biomass and mineral particles has shown enhanced capacity for the immobilization of metal ions, radionuclides, and organic pollutants, which can be applied in bioremediation technologies (Kadoshnikov et al., 1999).

Thus, soil type, particularly the content of clay minerals and organic matter, directly influences the stability, solubility, and functional activity of melanin. Due to its structural similarity to humic substances, melanin has the potential for long-term retention in soil, especially in clay-rich and organically enriched horizons, making it a promising agent in environmental technologies for soil protection.

In the case of Ukraine, particular attention should be given to soil restoration within destroyed settlements and damaged infrastructure zones, where elevated levels of heavy metals and explosive residues have been documented. Local pilot projects involving fungal consortia or melanin-based biomaterials could serve as initial models for scaling up biotechnological solutions in post-war recovery efforts.

Among the most effective strategies for employing melanin-producing organisms are the following: direct inoculation of melanin-producing strains into contaminated environments to establish localized bioprotective barriers; enzymatic biosynthesis of melanin *in vitro* followed by its application as a sorbent; and genetic modification of strains to enhance pigment production and increase tolerance to environmental stressors (Pavan et al., 2019; Tran-Ly et al., 2020).

White-rot fungi, such as *Phanerochaete chrysosporium* and *Trametes versicolor*, are capable of synthesizing melanin in the presence of heavy metals, a process accompanied by the activation of laccase and manganese-dependent peroxidase enzymes (Baldrian, 2003). This enables the simultaneous degradation of organic xenobiotics and stabilization of metals in soil or water. Comparable effects have been observed during the cultivation of *Pleurotus ostreatus* and *Stereum hirsutum* in media with high concentrations of cadmium and copper; these fungi accumulated significant amounts of metals and exhibited morphological and physiological adaptations to contamination stress (Baldrian, 2003).

At the same time, bacterial genera such as *Bacillus*, *Pseudomonas*, and *Streptomyces* have demonstrated the ability to synthesize pyomelanin- and eumelanin-type pigments. Particularly notable are polyketide synthase pathways, which enable melanin production without the need to supplement the medium with tyrosine or DOPA (Pavan et al., 2019). These microbial systems can be adapted for use in biofermentation platforms, opening the door to large-scale melanin biosynthesis from waste materials or low-cost substrates (Fomina and Gadd, 2014).

In the context of post-war environmental recovery, the use of melanin-producing microorganisms as part of integrated biotechnological strategies, for stabilizing heavy metals, reducing the toxicity of explosive residues, and protecting soil microbiomes holds considerable practical value. However, the implementation of such approaches requires further investigation, particularly field trials to evaluate the ecological competitiveness of melaninogenic strains in real-world ecosystems (Pavan et al., 2019; Tran-Ly et al., 2020).

Despite melanin‘s strong potential for binding heavy metals, radionuclides, and organic toxicants, its practical application in soil bioremediation faces several challenges. The main limitations include its resistance to degradation, limited mobility within the soil matrix, and high production costs, all of which complicate large-scale deployment.

Melanin is characterized by exceptional chemical stability, attributed to its polyaromatic structure, high degree of polymerization, and the presence of phenolic and indolic monomers. Its catabolism requires energy-intensive oxidative enzymes, which are rarely present in soil microbial communities (Guo et al., 2023). As a result, melanin is considered a recalcitrant compound and demonstrates substantial resistance to microbial breakdown (Fernandez and Kennedy, 2018). For instance, studies on mycorrhizal necromass have shown that high melanin content significantly slowed the decomposition of organic matter, even over two years (Fernandez et al., 2019). Similar findings were reported in (Linhares and Martin, 1978), where experiments with ^{14}C-labeled fungal melanin revealed that only 4–13% of the carbon was released as $^{14}CO_2$ after 12 weeks of soil incubation, levels comparable to the stability of humic acids.

Another major challenge is the limited mobility of melanin in soils. This is attributed to its low solubility and strong affinity for both mineral and organic soil components. As a result, melanin is rapidly adsorbed, especially in clay-rich soils and humic substances (Linhares and Martin, 1978). This leads to its activity being restricted to the zones of application, making it difficult to achieve uniform distribution across contaminated areas. Even with encapsulation or the use of carriers (e.g., biopolymeric matrices), consistent application of melanin under field conditions remains technically challenging (Singh et al., 2021).

The formation of biomineral sorbents based on fungal biomass and mineral particles has shown an enhanced capacity for the immobilization of metal ions, radionuclides, and organic pollutants, which can be applied in bioremediation technologies (Kadoshnikov et al., 1999).

From an ecological standpoint, the long-term presence of melanin in soils may have both beneficial and unintended consequences. On one hand, melanin facilitates the long-term immobilization of metals; on the other, its accumulation, or that of its complexes with trace elements, may influence nutrient availability for plants or alter the composition of soil microbial communities (Drewnowska et al., 2015). Furthermore, interactions between melanin and metal hydroxides or organic acids may result in the formation of novel, non-native soil complexes, complicating the prediction of long-term environmental outcomes (Paim et al., 1990; Knicker, 2004).

Another critical challenge is the high cost of melanin production. Although natural producers exist, melanin biosynthesis involves prolonged fermentation processes, requires specific nutrient media, and necessitates complex purification steps, all of which substantially increase production costs (Drewnowska et al., 2015). Experimental approaches, such as the production of water-soluble melanin-like pigments from *Bacillus weihenstephanensis*, highlight the potential of alternative biosynthetic routes (Drewnowska et al., 2015). However, these technologies are not yet scalable for field applications. Other limitations include the low yield of melanin per unit of biomass, the difficulty of extraction due to its poor water solubility, and the considerable structural heterogeneity of the pigment (Singh et al., 2021; Guo et al., 2023).

In the context of post-war recovery, particularly in areas of Ukraine contaminated with residues of explosives and heavy metals, melanin may be considered a promising component of bioprotective coatings or sorbents. However, its large-scale application is unlikely due to limited availability, high production costs, and the requirement for thorough incorporation into the soil. At present, more realistic applications involve localized interventions, such as melanin-based filtration systems or biomaterials for soil stabilization at sites of intense contamination (Falade et al., 2016; Fernandez and Kennedy, 2018).

Therefore, despite melanin's unique physicochemical properties, its widespread use in soil remediation remains limited by low bioavailability, technical challenges in application, and economic infeasibility. To expand its practical potential, future efforts should focus on optimizing biosynthesis, reducing purification costs, and developing efficient methods for encapsulation and targeted soil delivery (Falade et al., 2016; Singh et al., 2021;Guo et al., 2023).

Integration with Other Remediation Approaches

The integration of melanin with other bioactive and chemotactic components opens new avenues for the development of multifunctional systems aimed at remediating contaminated environments. Its ability to bind heavy metals, its antioxidant activity, and its stability across a wide range of conditions make melanin an ideal candidate for combined remediation strategies. However, achieving high efficiency typically requires melanin to act synergistically with other agents such as enzymes, polymer matrices, microorganisms, or synthetic components.

One of the most promising approaches involves incorporating melanin into electrically conductive polymer membranes, where it serves as an active component for heavy metal sorption. According to Tran-Ly et al. (2020), such membranes demonstrated effective removal of Pb^{2+}, Cd^{2+}, and Ni^{2+} from water, while maintaining mechanical stability and providing a high surface area for adsorption. This approach enhances remediation efficiency by ensuring stable immobilization of melanin and protecting its functional groups.

The combination of melanin with other bioactive compounds, particularly antioxidants, has also demonstrated significant potential. According to Zhang and Yang (2010), the co-application of melanin with glutathione and ascorbic acid enhanced the tolerance of *Sedum alfredii* H. to cadmium toxicity. The synergistic effect of these compounds reduced free radical levels in the leaves and boosted the activity of antioxidant enzymes, underscoring melanin's role as an intracellular modulator of protective mechanisms.

Further research highlights the effectiveness of hybridizing melanin with inorganic nanoparticles. Notably, Xie et al. (2020) synthesized a melanin/TiO_2 composite that, under visible light, enabled simultaneous photodegradation of dyes and reduction of Cr(VI). This demonstrates the potential of melanin in the integrated treatment of organic and inorganic water pollutants. In this context, melanin acts as an energy sensitizer, enhancing the photocatalytic properties of the host material.

In the field of bioremediation, growing attention is being given to the ability of fungi to synthesise melanin extracellularly under heavy metal stress. Oh et al. (2021) describe the extraction of melanin from *Amorphotheca resinae* cultures, enabling its non-contact application for wastewater treatment. The same study demonstrated that melanin is capable of forming stable complexes with heavy metals within microbially induced mineral matrices, which can be immobilized in soils or slags, forming long-lasting sorptive barriers.

Such systems can also function under conditions of radiation or ionic stress. For instance, Fomina and Gadd (2014) demonstrated the ability of melanin-based composites to protect surfaces from microbial colonization, opening up possibilities for their use not only in environmental remediation but also in the development of antimicrobial coatings.

Furthermore, Zaimenko (2023) suggested a three-step approach for soil rehabilitation which utilises melanin-synthesising microorganisms. At the first stage, the potential fertility of soils is assessed using indicators such as the abundance of melanin-containing micromycetes, laccase activity, and the content of labile and stable humus fractions. The second stage involves forming a structural matrix through the application of silicon-containing mixtures, which optimize the soil's agrophysical, agrochemical, and biological characteristics. The third and final stage is phytoremediation using plants capable of barrier-free accumulation of contaminants.

Overall, the synergy between melanin and other technologies or components enhances remediation efficiency, improves stability under harsh conditions, and adds novel functionalities – from photocatalysis to antibacterial activity. Future research should focus on optimizing these hybrid systems for widespread practical implementation across various ecosystems.

To improve melanin's stability and availability in soil systems, composite materials such as melanin-chitosan and melanin-alginate hydrogels are being developed (Sun et al., 2021). Recent research highlights the potential of microalgal-derived melanin as a component of soil enhancers, alongside other bioproducts such as carotenoids and fatty acids, for agricultural applications (Bhalamurugan et al., 2018). Microalgal melanin is characterized by a high content of functional groups that confer strong sorptive properties. These materials can be derived from residual biomass after bioenergy production, making them economically viable.

Thus, melanin-based soil amendments hold multifaceted potential, from soil remediation to reducing the environmental footprint of agricultural production. Nevertheless, key challenges remain, including scalability, uniform field-level distribution, bioavailability, and the assessment of long-term impacts on soil ecosystems (Roy and Rhim, 2021; Singh et al., 2021)

Conclusions

The full-scale invasion of Ukraine has caused extensive damage to soils, calling for effective and scalable solutions for their restoration. Traditional remediation methods are often too limited or resource-intensive to meet the scale of this challenge. Melanin, a naturally occurring biopolymer, shows strong potential for use in soil rehabilitation due to its stability, ability to bind heavy metals, antioxidant properties, and persistence in the environment. Melanin is produced by various soil microorganisms and accumulates through the decomposition of organic matter, including in conflict zones. It plays multiple roles in soil systems, including contaminant immobilization, carbon stabilization, and protection of microbial life under stress. Potential applications include the use of melanin-producing microbes or melanin-based materials to improve soil quality and reduce pollution. However, further research is needed to understand how to apply melanin effectively in different soil types, manage ecological impacts, and ensure cost-efficient production at scale. With continued study and thoughtful implementation, melanin could become an important tool in restoring war-damaged soils and supporting long-term ecological recovery. Its efficacy may be further enhanced through combined applications with other soil amendments, particularly silicon-based compounds, which can synergistically improve soil structure, nutrient availability, and plant stress tolerance, offering a holistic approach to rehabilitation.

Conflicts of Interest

The authors declare no conflict of interest.

Ethical Statement

This article doesn't contain any studies that would require an ethical statement.

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