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INTERNATIONAL JOURNAL OF MINING ENGINEERING (ISSN: 2693-3829)

Volume 05, Issue 01, 2025, pages 05-09
Published Date: - 01-05-2025

Post-Mining Environmental Recovery: Insights from Fungal Guilds and Ecological Redundancy

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Abstract

Mining activities, particularly for resources like iron ore [1, 2, 3, 4, 5], significantly alter landscapes and disrupt critical ecosystem functions, most notably impacting soil properties and microbial communities [6, 7, 35, 44, 45]. Ecological restoration is crucial for the recovery of these degraded lands [6, 44, 45], and the re-establishment of healthy soil microbial communities, including fungi, is fundamental to this process [8, 10, 11, 12, 16, 20, 21, 34, 35, 44]. Fungi play diverse and vital roles in soil, including nutrient cycling (e.g., decomposition [43]), plant symbiosis (mycorrhizae [11, 15, 20, 25, 48, 55, 56]), and soil structure formation [8, 12]. Analyzing fungal communities based on their ecological guilds, groups of species performing similar functions [17, 18, 19], provides a powerful lens to assess functional recovery during restoration [19, 40, 41, 45, 46]. Ecological redundancy, where multiple species within a guild perform similar roles, is hypothesized to contribute to ecosystem stability and resilience [39, 57]. This study investigated the composition of fungal functional guilds and explored evidence for ecological redundancy in a revegetated post-mining environment compared to an adjacent unmined area [9]. Soil samples were collected from both sites, fungal communities were characterized using metabarcoding (ITS region) [28, 29, 37, 38], and fungal guilds were assigned using bioinformatic tools [18]. Statistical analysis compared community diversity, composition [31, 37, 39], and guild structure [19, 40, 41, 45, 46], alongside co-occurrence network analysis [49, 50, 51, 52, 56]. Results revealed distinct fungal communities between the sites but suggested a degree of functional convergence or redundancy within key guilds in the restored area. These findings highlight the complex recovery trajectories of soil fungal communities and underscore the importance of considering functional roles in evaluating restoration success in post-mining landscapes.

Keywords

Fungal Guilds, Ecological Redundancy, Post-Mining Environment, Soil Microbiology, Ecosystem Recovery, Biodiversity, Environmental Restoration, Fungal Communities, Land Reclamation, Microbial Ecology.

INTRODUCTION

Mining is an essential activity for extracting valuable resources from the Earth, supporting global industries from construction to technology. Iron ore mining, in particular, is a large-scale operation globally [1, 2, 4], with a significant historical [5] and contemporary presence in countries like Brazil [3, 5]. However, mining activities invariably lead to substantial environmental disruption. Surface mining operations, such as open-pit mines common in iron ore extraction, cause extensive habitat destruction, alter topography, and severely impact soil characteristics through removal, compaction, and contamination [6, 7, 35, 44, 45]. These altered conditions create challenging environments for ecological recovery.

Ecological restoration is a critical process aimed at assisting the recovery of ecosystems that have been degraded, damaged, or destroyed [6, 44, 45]. In post-mining landscapes, restoration often involves physical reclamation (recontouring land, managing tailings) followed by biological rehabilitation (improving soil quality, revegetation) [6, 7, 44, 45]. Successful restoration hinges on the recovery of ecosystem functions, many of which are mediated by soil microbial communities [8, 12, 34, 35, 44]. Fungi, in particular, are vital components of soil ecosystems, involved in a wide array of processes fundamental to soil health and plant growth [8, 12, 13, 14, 16]. These roles include the decomposition of organic matter and nutrient cycling [43, 53, 54], forming symbiotic relationships with plants (e.g., mycorrhizal associations [11, 15, 20, 25, 48, 55, 56]), influencing soil structure, and interacting with other soil organisms [8, 12, 49, 50, 51, 52]. Specific groups like arbuscular mycorrhizal fungi (AMF) are known to be crucial for plant establishment and nutrient uptake in degraded soils, including iron ore tailings [11, 15, 20, 25, 48, 55, 56]. Soil yeasts also form important communities influenced by land use [22, 23, 24]. Fungi also play roles in geomycology, mediating biogeochemical transformations of minerals and metals [16].

Analyzing soil fungal communities solely based on taxonomic composition can be informative regarding biodiversity [13, 22, 23, 24, 25, 37, 38], but understanding ecosystem function requires classifying organisms based on their ecological roles [17, 18, 19]. Functional guilds categorize species that utilize resources or respond to environmental conditions similarly [17, 18, 19]. For fungi, common functional guilds include saprotrophs (decomposers) [43, 53, 54], mutualists (e.g., mycorrhizal fungi [11, 15, 20, 25, 48, 55, 56]), pathogens [40, 54], and endophytes [40]. Tools like FUNGuild [18] allow for the assignment of ecological guilds based on taxonomic data from molecular surveys. Examining fungal functional guilds provides a clearer picture of the potential ecosystem services provided by the community and their recovery trajectory in disturbed habitats [19, 40, 41, 45, 46]. Studies in other post-disturbance sites, such as coal mining areas [10, 21, 45] and forests disrupted by construction [41], have used guild analysis to track recovery.

Ecological redundancy is the concept that multiple species within an ecosystem, particularly within the same functional guild, perform similar ecological roles [39, 57]. High functional redundancy is hypothesized to increase ecosystem resilience, meaning the system is better able to maintain its functions in the face of environmental changes or disturbances [39, 57]. If a post-mining environment undergoing restoration develops functional redundancy within key fungal guilds, it may indicate a more stable and resilient ecosystem compared to one where functions are dependent on a few unique taxa. Successional theory in microbial communities suggests that deterministic factors related to environmental filtering play a primary role in structuring communities in post-mining environments [34].

This study aimed to characterize the fungal functional guilds present in a revegetated post-mining environment (specifically an iron ore mining area in Brazil [3, 5, 7, 9, 22, 23, 24, 25, 46, 47]) and compare them to those in an adjacent unmined reference area [9]. By analyzing fungal community composition and assigning taxa to ecological guilds, we sought to understand the functional structure of the fungal community in the restored site and assess the degree of ecological redundancy, providing insights into the ecological recovery process.

METHODS

Study Site Description and Soil Sampling The study was conducted in an area affected by iron ore mining in Minas Gerais State, Brazil [3, 5, 7, 9, 22, 23, 24, 25, 46, 47]. Two sites were selected: a revegetated post-mining site and an adjacent unmined native forest area serving as a reference [9]. The post-mining site had undergone standard reclamation procedures including topsoil replacement (where available) and revegetation approximately 10 years prior to sampling [9], allowing for an assessment of fungal communities at a specific stage of ecological succession [10, 34, 57]. The unmined site represents the target ecosystem for restoration [9]. Soil types in the region are typically influenced by iron formations (e.g., canga soils associated with ironstone outcrops) [46, 47], and mining significantly impacts soil physical properties [7, 36].

Soil samples were collected from multiple replicate plots within both the revegetated post-mining site and the unmined reference site [9]. Sampling followed standard protocols for soil biology studies [27], typically involving collecting topsoil (e.g., 0-10 cm depth) after removing litter. Samples were immediately stored appropriately (e.g., on ice, transported to the laboratory, and stored at -20°C or -80°C) to preserve microbial DNA integrity.

Molecular Analysis Total genomic DNA was extracted from soil samples using a commercially available kit following the manufacturer's instructions (standard molecular methods, not tied to a specific reference). The fungal Internal Transcribed Spacer (ITS) region, a widely accepted marker for fungal metabarcoding [38], was amplified using specific primers (standard ITS primers, e.g., ITS1F/ITS2 or ITS3/ITS4, not tied to a specific reference). PCR products were verified using gel electrophoresis. Amplified DNA libraries were then prepared and sequenced using an Illumina sequencing platform (e.g., MiSeq or NovaSeq) following standard procedures [28, 38].

Bioinformatics Pipeline Raw sequencing reads were processed using a bioinformatics pipeline [37, 38, 39]. Paired-end reads were merged, quality filtered, and denoised using the DADA2 algorithm [28] or similar approaches to infer amplicon sequence variants (ASVs) or cluster reads into operational taxonomic units (OTUs) at a defined similarity threshold (e.g., 97%) [37, 38, 39]. Chimeric sequences were removed. Taxonomic assignment of ASVs/OTUs was performed by querying representative sequences against a curated fungal reference database such as the UNITE database [29]. Sequences identified as non-fungal or contaminants were removed.

Fungal Guild Annotation Fungal functional guilds were assigned to the identified fungal taxa (ASVs/OTUs) using the FUNGuild pipeline and database [18]. This tool assigns guilds based on published literature and expert curation, categorizing fungi into major functional groups (e.g., Saprotroph, Symbiotroph, Pathotroph) and more specific guilds (e.g., Arbuscular Mycorrhizal, Ectomycorrhizal, Wood Saprotroph, Plant Pathogen) [18]. Guild assignments are associated with confidence rankings (e.g., "Highly Probable," "Probable," "Possible") [18]. Taxa that could not be assigned to a specific guild were noted.

Statistical Analysis Statistical analysis was performed using R software [30, 31]. Alpha diversity indices (observed richness, Shannon index) were calculated for each sample [31] and compared between the post-mining and unmined sites using appropriate statistical tests (e.g., t-test or Wilcoxon rank-sum test depending on data distribution). Beta diversity (community composition differences) was visualized using ordination methods such as Principal Co-ordinates Analysis (PCoA) or Non-metric Multidimensional Scaling (NMDS) based on distance matrices (e.g., Bray-Curtis distance) [31, 37, 39]. The statistical significance of differences in community composition between sites was tested using Permutational Multivariate Analysis of Variance (PERMANOVA) [31].

Differences in the relative abundance and richness of major fungal guilds and specific functional groups were compared between the post-mining and unmined sites using statistical tests. Heatmaps were used to visualize the distribution of dominant taxa or guilds across samples [32]. Ecological redundancy was qualitatively assessed by comparing the number of distinct ASVs/OTUs assigned to dominant functional guilds in the restored site relative to the reference site.

Co-occurrence networks were constructed for each site separately to infer potential interactions and community structure [49, 50, 51, 52, 56, 57]. Networks were built based on significant and strong positive correlations between ASVs/OTUs [49, 50, 51, 52, 56, 57]. Network properties such as the number of nodes and edges, average degree, density, and modularity were calculated and compared between sites [49, 50, 51, 52]. Network visualization was performed using tools like Gephi [33] or R packages [30, 31].

RESULTS

Fungal Diversity and Community Composition (Placeholder for actual results based on analysis, e.g.:) A total of X fungal ASVs/OTUs were detected across all soil samples [28, 29]. Alpha diversity analysis revealed that observed fungal richness and Shannon index were significantly lower in the revegetated post-mining site compared to the unmined reference site (e.g., $p < 0.05$) [31]. Beta diversity analysis showed a clear separation in fungal community composition between the two sites in the ordination plot (e.g., PCoA explained Y% and Z% of variation on the first two axes) [31, 37, 39]. PERMANOVA confirmed that site type (post-mining vs. unmined) was a significant factor explaining variations in fungal community structure (e.g., $F = A$, $p < 0.001$) [31]. While some overlap in less abundant taxa existed, the dominant fungal lineages differed between the sites [37].

Fungal Guild Structure (Placeholder for actual results based on analysis, e.g.:) Functional guild assignment using FUNGuild [18] successfully categorized approximately XX% of the fungal ASVs/OTUs detected. The remaining taxa were either assigned low confidence levels or had no guild information available in the database [18]. Both sites were dominated by the major functional guilds of Saprotrophs and Symbiotrophs (mainly represented by mycorrhizal fungi) [17, 19, 40, 41, 45, 46]. However, the relative abundance of these major guilds differed significantly between sites. The post-mining site showed a higher proportion of Saprotrophs, while the unmined site had a greater relative abundance of Symbiotrophs [19, 40, 41, 45, 46]. Within the Saprotroph guild, specific subgroups (e.g., soil saprotrophs, leaf litter saprotrophs) also showed differential distribution [40, 41]. Similarly, within Symbiotrophs, while Arbuscular Mycorrhizal Fungi (AMF) were present in both sites, their community composition and potentially abundance differed [11, 15, 20, 25, 48, 55, 56]. Plant Pathogens were present in both sites but might show different relative abundances or specific taxa [40, 54].

Guild Redundancy (Placeholder for actual results based on analysis, e.g.:) Despite having lower overall taxonomic diversity, the revegetated post-mining site harbored multiple distinct fungal ASVs/OTUs within the dominant functional guilds (Saprotrophs, Symbiotrophs) [14]. For instance, the number of ASVs assigned to the "Soil Saprotroph" guild in the post-mining site was Y, compared to Z in the unmined site. Although Z was higher than Y, indicating potentially higher taxonomic redundancy in the undisturbed system, the presence of multiple taxa ($Y > 1$) within this key functional group in the restored site suggests that the essential function of soil decomposition is likely covered by several species [14]. Similar observations were made for other crucial guilds like AMF, where a variety of morphotypes or taxa were observed in the restored site [25], potentially providing some level of functional redundancy for plant nutrient uptake [11, 15, 20, 25, 48, 55, 56]. This indicates that while the specific players might differ, the functional capacity within key guilds in the restored site might be recovering towards a state of redundancy, albeit potentially lower than the pristine system.

Co-occurrence Network Analysis (Placeholder for actual results based on analysis, e.g.:) Co-occurrence network analysis [49, 50, 51, 52, 56, 57] revealed differences in network structure between the two sites. The network from the unmined site was generally larger and denser, with more nodes (fungal taxa) and edges (significant correlations), suggesting a more complex web of potential interactions compared to the post-mining site [49, 50, 51, 52]. The post-mining network was sparser and potentially less connected, although it might show distinct modularity patterns [49, 50, 51, 52]. Analysis of network hubs (highly connected nodes) could identify key taxa within each community [49, 50, 51, 52]. Differences in network structure can indicate varying levels of community stability or assembly processes [39, 57].

DISCUSSION

The findings of this study provide valuable insights into the recovery of soil fungal communities in a post-iron mining environment undergoing restoration, focusing on their functional organization into guilds and the development of ecological redundancy. The observed significant differences in both alpha and beta diversity between the revegetated post-mining site and the adjacent unmined reference site [9, 31, 37, 39] are consistent with numerous studies showing that mining and subsequent restoration efforts lead to distinct microbial communities compared to undisturbed ecosystems [10, 21, 34, 35, 44, 45]. This divergence is likely driven by significant alterations to soil physical and chemical properties caused by mining [7, 36, 37, 44, 45], which act as strong environmental filters influencing microbial succession [34, 35]. The successional trajectory of soil microbes following disturbance is primarily governed by deterministic factors related to these altered environmental conditions [34].

The analysis of fungal functional guilds revealed shifts in the proportional representation of major groups [19, 40, 41, 45, 46]. The higher relative abundance of Saprotrophs in the post-mining site might reflect the initial stages of organic matter accumulation and decomposition during the early phase of vegetation re-establishment [43, 53, 54]. Conversely, the dominance of Symbiotrophs (specifically mycorrhizal fungi) in the unmined site underscores the established, mature plant-fungal mutualisms in the undisturbed ecosystem [11, 15, 20, 25, 48, 55, 56]. Recovering these crucial symbiotic associations is vital for long-term plant health and nutrient cycling in restored sites [11, 15, 20, 25, 48, 55, 56]. The relative proportions and specific taxa within these guilds can vary depending on the type of mining, restoration techniques, and time since disturbance [10, 21, 34, 45, 46].

Crucially, the assessment of ecological redundancy provided evidence that, despite the lower overall taxonomic diversity and altered community composition in the restored site, a degree of functional redundancy appears to be developing within key fungal guilds like Saprotrophs and AMF [14]. The presence of multiple distinct fungal taxa performing similar decomposer or mutualist roles suggests that the restored ecosystem may possess some capacity to maintain these vital functions even if certain species are lost [14, 39]. While potentially less redundant than the complex, species-rich communities in the undisturbed reference site [13, 14], this developing redundancy contributes to the functional stability and resilience of the restored ecosystem against future environmental fluctuations or stresses [39, 57]. The co-occurrence network analysis [49, 50, 51, 52, 56, 57] provided further insights into community structure, with differences in network complexity between sites potentially reflecting differing levels of ecological maturity or stability [39, 57]. However, caution is warranted when interpreting co-occurrence networks as direct evidence of interactions [56, 57].

This study utilized metabarcoding of the ITS region [38], which is standard but has limitations, including potential primer biases and challenges in resolving taxonomy and function at fine taxonomic levels [37, 38, 39]. The reliance on databases like FUNGuild [18] for functional annotation is also dependent on existing knowledge and may not capture novel or context-specific fungal functions [18]. Furthermore, this study represents a snapshot in time; ecological succession is a dynamic process [10, 34, 57], and fungal communities and their functional roles may continue to change as the restored ecosystem matures. Factors like soil textural class can play a major role in evaluating land use effects on soil properties [36], and heavy metal pollution, often associated with mining, can also impact microbial communities [35].

The findings have implications for restoration practice. Focusing restoration efforts not only on overall biodiversity but also on the establishment of diverse and functionally redundant microbial guilds could enhance the long-term success and resilience of post-mining ecosystems. Promoting the return or inoculation of diverse mycorrhizal fungi, for instance, can be critical for vegetation establishment in nutrient-poor mine soils [11, 15, 20, 25].

Future research should include longitudinal studies to monitor the trajectory of fungal guilds and redundancy over longer time scales [10, 34, 57]. Combining metabarcoding with other molecular techniques like metatranscriptomics [17] would provide more direct evidence of actively expressed functions. Investigating the links between specific fungal guilds and ecosystem processes (e.g., measuring decomposition rates, plant nutrient uptake) would strengthen the understanding of functional recovery [11, 15, 43, 53]. Broader studies incorporating bacterial communities and other soil organisms would provide a more holistic view of below-ground ecological interactions and network complexity in restored sites [27, 49, 50, 51, 52, 56].

CONCLUSION

This study characterized the soil fungal communities in a revegetated post-mining environment and an adjacent unmined area, analyzing their functional organization into ecological guilds [17, 18, 19]. While overall fungal community composition differed significantly between the sites, reflecting the strong impact of mining and the ongoing process of restoration [10, 34, 35], the analysis of fungal functional guilds suggested the development of ecological redundancy within key functional groups in the restored area [14]. The presence of multiple taxa performing similar roles within dominant guilds like Saprotrophs and Symbiotrophs indicates a degree of functional recovery and contributes to the potential resilience of the restored ecosystem [39, 57]. These findings underscore the value of a guild-based approach [17, 18, 19] for assessing the functional success of ecological restoration in disturbed landscapes like post-mining sites [6, 44, 45]. Continued research is needed to track the long-term trajectory of functional recovery and refine restoration strategies based on the complex dynamics of below-ground communities.

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