Fungal Applications for Forest Management and Restoration

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Table of Contents

Abstract

Fungi can play an important role in ecological restoration and forest sustainability efforts. Degraded lands, invasive plants, and post-wildfire conditions are challenges that forest managers face, and the limited attention given to fungi may be a reason for the failure of restoration efforts. The use of arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF) as restoration tools can lead to future restoration initiatives that surpass past failures. AMF and EMF play pivotal roles in increasing soil attributes, seedling/shrub establishment and survival, and plant community succession. EMF have been shown to promote host plant success under heavy metal toxicity by creating physical barriers between heavy metals and plant symbionts, uptaking heavy metals in their sporocarps, and making these compounds bioavailable. Retention forestry and soil transplants from mature forests are methods used to minimize damage to the EMF community and promote seedling establishment and growth after clear cutting. Native and healthy AMF and EMF communities can prevent invasive plant invasions, but if avoidance or prevention is not possible, EMF inoculation can be successful in promoting native plant establishment in restoration efforts. Although, this would require the removal of invasive plants prior to treatment. Mycopesticides have been shown to be effective in the management of insect pests and in some instances, combat insecticide resistance. Mycopesticides are also multifaceted in their approach to insect management as they can also assist in activating plant defenses, attracting natural enemies, and parasitizing micro-symbtions. Similarly, mycoherbicides have been shown to be effective when directly applied for the control of invasive plants in some cases. They may also collude with multiple species of mycoherbicides or chemical herbicides to produce the desired effects. Their bioactive metabolites also produce naturally derived herbicides, which are more potent than direct applications. In summary, this review highlights the importance of fungi in sustainable forest management and develops a collection of effective fungal applications that can be used to support future restoration initiatives. By incorporating these practices, forest managers can improve ecological restoration efforts and promote forest sustainability.

This paper is formatted for the *Journal of Forestry*, with a word limit of 6000. This paper exceeds that but there was an effort to limit the length of the manuscript.

Introduction

In forest management, fungi play a crucial role in maintaining forest health and productivity. For example, forest managers can use fungi as bioindicators to assess the health of a forest ecosystem (Folke and Knudsen 1994; Laganà et al. 2002; Gadzala-Kopciuch et al. 2004). Fungi are sensitive to changes in the forest environment, and shifts in fungal communities can indicate disturbances such as pollution, climate change, or deforestation (Jovan 2008; Zheng et al. 2017). Additionally, forest managers can use fungi as biocontrol agents to manage forest pests and diseases. Fungi have natural mechanisms that can help control forest pathogens, and some fungi can be cultivated and used to protect plants from disease. In summary, fungi are an essential component of forest ecosystems, and their use in forest management is critical to maintaining forest health and productivity. Understanding the role of fungi in forest ecosystems and how to use them in forest management is essential for ensuring the sustainability of our forests.

The literature on the utilization of fungi in forest management is currently limited. There are numerous studies that examine how forest management affects fungi (Blaser et al. 2013; Goldmann et al. 2015; Tomao et al. 2020); however, comprehensive studies on the various uses of fungi in forest management are lacking (Auld 1990; Wall et al. 1992; Stamets 2005). Therefore, the purpose of this review is to provide a comprehensive overview of the applications of fungi to highlight their versatility and benefits as forest management tools. In addition to discussing common topics of fungal applications, this review aims to bring attention to other potential uses of fungi that have not been widely studied. In total, this review can serve as a valuable resource for researchers and practitioners in the field of forest management.

To begin, what are fungi?

Fungi constitute a diverse group of organisms in the kingdom fungi (Zanne et al. 2020; see also Moore et al. 2020; Watkinson et al. 2016) that are fundamental to most ecosystems (Zanne et al. 2020). These unique organisms have various roles in the natural world, including functioning as decomposers, mutualists, and pathogens. By breaking down organic matter, fungi recycle nutrients and help to maintain soil health, thereby promoting tree growth and general forest health. Furthermore, many fungi have symbiotic relationships with trees, forming mycorrhizal associations that enhance nutrient uptake and disease resistance. Therefore, fungi play a crucial role in sustaining forest ecosystems and should be viewed as a crucial component of forest management.

Mycorrhizal fungi, which are associated with approximately 90% of terrestrial plants (Watkinson 2016), are crucial plant symbionts (Figure 1). Mycorrhizal fungi transport essential nutrients to the roots of their plant partners, in exchange for photosynthates. Root and mycorrhizal networks extend deep into the soil and connect with other plants. Two main types of mycorrhizal fungi exist in forest ecosystems: ectomycorrhizal fungi (EMF) and arbuscular mycorrhizal fungi (AMF). EMF mainly belong to the phyla Basidiomycota and Ascomycota (Luo et al. 2014; Zanne et al. 2020), while AMF belong to the phylum Glomeromycota (Fernandes et al. 2021). EMF establish external root connections with their plant partners, while AMF create intracellular organs called arbuscules within the plant partner's root cells for resource sharing. EMF are the most significant contributors to carbon sequestration within forests. According to Watkinson (2016), an estimated 10-20% of the host plant's photosynthate is allocated to its EMF mycelium. Yin et al. (2014) found that different amounts of carbon root exudates were displayed by tree-associated mycorrhizae, depending on whether they were associated with AMF or EMF. EMF associations were found to contribute more than AMF associations (Yin et al. 2014). Carbon cycling that takes place within mycorrhizal fungi provides approximately half of the energy required for belowground microbial life (Boddy 2016a), making these fungi critical components of forest ecosystems.

Figure 1. Primary functions of mycorrhizal fungi that benefit their host plants and soil processes. SOM means ‘soil organic matter’. Created by KP.

Saprotrophs are fungi that decompose organic matter and play vital roles in nutrient cycling (Boddy 2016a). Saprotrophs are found among all fungal lineages (Zanne et al. 2020), but commonly belong to the phyla Basidiomycota or Ascomycota (Eichlerová et al. 2015).

Saprotrophs break down organic matter and soil litter, which helps maintain nutrient levels within forests (Zanne et al. 2020). Forest litter decomposers and wood decomposers, such as brown, white, and soft rot fungi, are examples of different types of saprotrophs (Eichlerová et al. 2015; Zanne et al. 2020). These fungi are essential players in decomposition networks and can break down complex molecules such as lignin and cellulose associated with wood (Boddy 2016a). Without decomposer fungi, the necessary carbon and minerals would be inaccessible in dead tree tissues, making it difficult for forests to function properly (Boddy 2016a).

Pathogenic fungi can be found in all fungal taxa but are primarily in the phyla Basidiomycota and Ascomycota (Łaźniewska et al. 2012; Zanne et al. 2020). These fungi act as plant pathogens and fall into two main categories: biotrophs and necrotrophs (Boddy 2016b; Harley 1971; Zanne et al. 2020). These pathogens derive energy from their hosts either obligately or facultatively (Boddy 2016b). While well-known examples such as Dutch elm disease (Karnosky 1979; Brazier 1991; Braier 2020) or potato blight (Cox and Large 1960; Austin Bourke 1964; Van der Waals et al. 2001) come to mind, not all fungal pathogens actively kill their host. Many plants are naturally resistant to fungal pathogens, and certain conditions (both internally from the host and externally by the pathogen and environment) must be present to successfully overcome this resistance (Boddy 2016b; Kumar M. et al. 2018; Łaźniewska et al, 2012). This balance between natural resistance and ideal infection conditions creates a predator-prey-like system that promotes biodiversity and maintains plant populations (Castello et al. 1995; Holah et al. 1997; Zanne et al. 2020). For instance, Holah et al. (1997) observed a fungal pathogen infecting Douglas-fir that created openings in the canopy and promoted biodiversity. Although fungal pathogens can become problematic in ecosystems, not all of them are a threat to forests. Thus, managing fungal outbreaks requires a nuanced approach that considers a particular pathogen and its ecological context.

Role of fungi in forest management practices

Forest management practices can maintain the health of forest ecosystems, promoting biodiversity, and ensuring the sustainable production of forest resources (FAO 2020). Thinning, the selective removal of trees, is used to promote tree growth, reduce competition for resources, and prevent catastrophic fires (Liang et al. 2018) but also affects plant-fungal associations (Tomao et al., 2020). Timber harvesting is another common practice that involves the removal of trees for wood products or other uses (Olson et al. 2018). Planting can be used to establish new trees or to restore degraded areas (Liang et al. 2017). Prescribed burns are planned fires that are used to reduce wildfire risk, promote ecosystem health, and restore natural fire regimes (Hart et al. 2018; Hart et al. 2005). Clear-cutting involves the removal of all trees in an area and is used to create space for new growth, often in conjunction with reforestation efforts (Kumar P. et al. 2018). Various restoration techniques can be used to rehabilitate degraded areas, such as removing invasive species, planting native species, and restoring soil health (Liang et al. 2017). Slash piles, which accumulate tree branches and other debris, can be used for fuel, compost, and erosion control (Olson et al. 2018). All of these practices can affect fungal diversity, growth, establishment and plant interactions. Some fungi can also be used to control forest pests and diseases, thereby reducing the need for chemical interventions (Petrini et al. 1993). However, it is important to recognize that fungi are also a natural part of forest ecosystems and should be protected and conserved along with other flora and fauna (Baker et al. 2015).

Effects of forest management on fungal communities

Understanding the impact of forest management practices on fungal communities is challenging due to variations in techniques and severity. For instance, a review conducted by Tomao et al. (2020) found that certain forest management practices, such as thinning, clear-cutting, and prescribed burning, can have adverse effects on fungal communities in ponderosa pine forests. Thinning, which promotes grass establishment, benefits AMF species, but can reduce EMF species diversity and richness (Korb et al. 2003; Overby et al. 2015). Clear-cutting can increase AMF communities, but it likely reduces EMF population and diversity (Overby et al. 2015; Hart et al. 2018). However, alternatives, such as retention trees, shelterwood, or selective cutting, which retain inoculated trees, can help reduce the negative impact on EMF diversity (Price 2021; Tomao et al. 2020).

Fire can be a significant factor for various forest types (Hart et al. 2018; Martínez de Aragón et al. 2012). In some forest types, like ponderosa pine, fire adaptation through fuel treatments and prescribed burns promote the health and productivity of these forests and reduce the risk of future catastrophic fires (Hart et al. 2018). Depending on the forest type, fire can have different impacts on the fungal community (Martínez de Aragón et al. 2012). For example, predicting the impact of fire on EMF in different forest types is dependent on chemical and physical factors before and after fire (Martínez de Aragón et al. 2012). In western conifer forests, low-severity burns promote fire-tolerant and arbuscular mycorrhizal fungi (AMF) species; however, high-severity burns can negatively affect fungal communities and drastically alter their composition (Filialuna and Cripps 2021; Glassman et al. 2016; Korb et al. 2003; Overby et al. 2015; Owen et al. 2019). Slash pile burns can concentrate heat on the soil surface, resulting in severe burns that decrease EMF species richness and likely negatively affect AMF diversity and survival in Ponderosa pine type forests (Esquilin et al. 2007; Reazine et al. 2016). Whereas in pinyon pine forest types, Haskins and Gehring (2004) determined there to be no significant impact on the AMF community. Therefore, it is important to use controlled burning techniques to maintain a balance between low-severity burns that promote forest health and fungal diversity while avoiding high-severity burns that can have negative impacts.

In summary, forest management practices, such as thinning, clear cutting, and prescribed burning, can have both positive and negative effects on fungal communities in forests. Thinning and clear cutting can benefit some fungal species but reduces the diversity and richness of others. Alternatives to clear-cutting, such as retention trees, shelterwood, or selective cutting, could help to reduce the negative impact on fungal diversity (Tomao et al. 2020). The reintroduction of low-severity fires is necessary to promote forest health and productivity; however, high-severity fires can negatively affect fungal communities and drastically alter their composition (Filialuna and Cripps 2021; Glassman et al. 2016; Korb et al. 2003; Overby et al. 2015; Owen et al. 2019). Prescribed burn techniques such as slash piles can also negatively affect the richness and diversity of some fungal species (Esquilin et al. 2007; Reazine et al. 2016) but leave no significant impact on others (Haskins and Gehring 2004) depending on forest type. It is important to note that the effect of forest management practices on fungal communities can vary depending on the forest type and specific management technique. Therefore, it is necessary to specify the type of forest and the specific management practices to obtain accurate results.

Fungal application

Mycopesticides

Climate change is expected to impact insect populations and plant defense (CITATION). Warmer temperatures and more frequent droughts are likely to increase insect populations and weaken plant defense mechanisms (Jactel et al. 2019). Although some impacts of climate change may mitigate these circumstances (Jactel et al. 2019), forest management needs to implement increased integrated pest management (IPM) to combat forest pests under these conditions. However, the use of chemical pesticides against agricultural insect pests is not a sustainable solution because of their harmful effects on the environment (Poveda 2021; Ortucu and Algur 2017). Consequently, alternative measures for controlling insect pests are becoming increasingly important. Mycopesticides, also known as entomopathogenic fungi (EPF), are natural and sustainable tools that can replace chemical pesticides (St. Leger et al. 1996). In light of these challenges, forest management must embrace sustainable and innovative pest management methods. This includes the use of IPM approaches that consider the impacts of climate change and rely on natural and sustainable solutions such as mycopesticides.

Mycopesticides are arthropod-killing fungi belonging to the EPF group (Litwin et al. 2020). There are a large variety of EPF species, whose main purpose in the environment is to control insect populations (Litwin et al. 2020). Some species of EPF are utilized in organic farming as biocontrol agents, but further research and understanding of these organisms could open the door for mainstream applications (Litwin et al. 2020). EPF species are diverse in their roles in the ecosystem and the ways in which they can protect plants from insect pests (Litwin et al. 2020; Poveda 2021). Many species of EPF are also plant endophytes that can physically attack insects and assist the plant in activating defenses against them (Litwin et al. 2020; Poveda, 2021). EPF penetrates the cuticle of insect prey to consume them internally (Litwin et al. 2020). However, some EPF can attract predatory insects and eliminate food sources for insect pests

(Poveda 2021). The different mechanisms by which EPF can aid in protecting plants make them a multi-use tool for combating insect pests (Table 1).

The current applications of mycopesticides are primarily studied for agricultural and human health concerns (Barbarin et al. 2017; Litwin et al. 2017; Ortucu and Algur 2017; Poveda 2021). This is because of the economic impact of insects in these fields. By understanding the mechanisms of mycopesticides in these applications, their use can be translated into forest management. Various applications of mycopesticides to control insect pests have been successful under appropriate environmental and time conditions (Barbarin et al. 2017; Ortucu and Algur 2017; Poveda 2021).

Case studies regarding Mycopesticides

Research on mycopesticide uses have revealed some beneficial effects. A study done by Barbarin et al. (2017) reported that insecticide-resistant and non-insecticide-resistant strains of bed bugs were effectively controlled by the application of *Beauveria bassiana*. All tested strains of bed bugs resulted in 95-99% mortality from *B. bassiana* after 14 days of treatment (Barbarin et al. 2017). Insecticide-resistant strains of bed bugs can have thicker cuticles as a result of their resistance, but *B. bassiana* infection and mortality from these strains were not affected (Barbarin et al. 2017). Further studies on the application of mycopesticides have also found evidence that their use can reduce insecticide resistance (e.g., Farenhorst et al. 2009; Barabin et al. 2017).

One genus of EPF, *Trichoderma*, is widely studied for its use as a mycopesticide in agriculture. Poveda (2021) compiled various studies of direct and indirect ways in which *Trichoderma* has successfully been used as a mycopesticide, finding different species of *Trichoderma* are used to control various insect species through direct parasitism, with success rates as high as 100% mortality in the respective insect pests (Poveda 2021). Some *Trichoderma* species also produce effective secondary metabolites, antifeedant compounds, and repellent metabolites (Poveda 2021). Direct impacts of antifeedant compounds and repellent and secondary metabolites have been reported to have between 50%-100% mortality rates in the respective insect pests (Poveda 2021). *Trichoderma* can also be utilized for its indirect effects, such as activating its plant-symbiont defense system, ability to attract natural enemies, and parasitism of microorganism symbionts (Poveda 2021). These defense mechanisms can be as significant as the direct control strategies employed by this genus. Silva et al. (2019) determined the inoculation of lanzone seedlings with *Trichoderma* spp. was correlated with the plants' production of jasmonic acid, salicylic acid and other phytochemicals. This stimulation to the lanzone seedlings' defenses displayed an overall resistance to the scale insect, *Lepidosaphes ulmi* (Silva et al. 2019). Compared to the control, *Trichoderma* treated seedlings had significantly lower and slower growing scale populations (Silva et al. 2019). The same defense activation caused by various species of *Trichoderma* have also been documented to attract predatory insects and parasitoids to aid in the biocontrol of the respective pest (Coppola et al. 2019; Poveda 2021). In one example of leaf cutter ants, *T. viride* parasitized the fungal food source of the colony and resulted in 100% mortality by starvation (Lopez and Orduz,2003). This treatment was also more effective in causing mortality than the chemical pesticide, pirimiphos methyl (Lopez and Orduz 2003). Lopez and Orduz (2003) also found 100% mortality in leaf cutter ants by the fungal agent, *Metarhizium anisopliae* (Metsch.) Sorokin. Overall, the various and diverse ways in which *Trichoderma* species can be utilized to combat insect pests is impressive. As a better understanding of fungal species is needed to harness their power in management, examples such as this give promise to just how powerful a weapon species of EPF can be in biocontrol.

A commonly used and well known mycopesticide, *Beauveria bassiana*, has been shown to be effective against some mites and forest insects in the orders of Coleoptera, Lepidoptera, and Hymenoptera (Ortucu and Algur 2017). Its effectiveness in parasitizing various species of insects makes it a promising substitute for chemical pesticides (Ortucu and Algur 2017). However, to create more consistently effective results, Ortucu and Algur (2017) compared two strains of *B. bassiana* to determine which would be best for use in IPM of the mite *Tetranychus urticae* Koch. Their study used isolates from a parasitized mite, and the parameters of their study focused on qualities identified as influential in the success of a mycopesticide, such as tolerance to UV radiation, tendency to mass produce, pathogenicity, and mycelial growth and sporulation at different temperatures (Ortucu and Algur 2017). UV radiation, temperature, and humidity can all influence the germination of fungal spores and, therefore, their infectivity (Ortucu and Algur 2017), and their ability to mass produce (Ortucu and Algur 2017) can be specificity limiting factors for commercial production (Brodeur 2012). However, *Beauveria* spp. have already been identified to infect a wide host range (Meyling et al. 2009). Their study was successful in identifying which strain was more UV-tolerant and produced more mycelial growth and sporulation under different temperatures, mass production, and virulence (Ortucu and Algur 2017). Strain AT076 produced the most virulent results as well as UV tolerance and mass production compared to the competing AT007 strain (Ortucu and Algur 2017). These results hold promise for the adaptation of *B. bassiana* to other insect pests. This is because by identifying the most appropriate climatic conditions, as well as the ecology of the strain and its pathogenicity against a targeted insect, managers could plan treatments efficiently. Although it is not necessarily feasible to test various strains against numerous insects, cultivating *B. bassiana* with the most ideal characteristics could strengthen its use as a mainstream mycopesticide.

With the risks of using chemical pesticides and the future encroachment of insect pests into forests affected by climate change, the need for a sustainable and effective alternative is becoming even more important. EPF has been shown to provide ample resources to combat forest insect pests (Barbarin et al. 2017; Coppola et al. 2019; Litwin et al. 2020; Lopez and Orduz 2003; Ortucu and Algur 2017; Poveda 2021; Silva et al. 2019). Overall, EPF offer a welcome alternative to chemical pesticides (St Leger et al., 1996) and may be the answer to sustainable IPM targeting insects in forests.

Table 1. Summary of direct and indirect applications of Mycopesticides and Mycoherbicides.

Management Application	Application Type	Fungal Application	Reference
Mycopesticides	Direct	Parasitism	Barbarin et al. 2017; Lopez and Orduz 2005; Poveda 2021
		Secondary/repellant metabolites	Poveda 2021
		Antifeedant compounds	Poveda 2021
	Indirect	Plant-symbiont defenses	Poveda 2021; Silva et al. 2019
		Attract natural enemies	Coppola et al. 2019; Poveda 2021
		Parasitism of microorganism symbiont	Lopez and Ordu, 2005; Poveda, 2021
Mycoherbicides	Direct	Parasitism	Bourdot et al. 2006; Gibson et al. 2014

		Combination application	Mitchell et al. 2008
	Indirect	Bioactive metabolites	Evidente et al. 2008a,b

Mycoherbicides

Forest management sometimes relies on the use of herbicides to control invasive plant species (The Nature Conservancy 2010). Invasive plants, especially when introduced, pose a serious threat to biodiversity (Müller-Schärer et al. 2004; Zenni and Ziller 2011). Similar to chemical pesticides, chemical herbicides also have negative effects on health and cause resistance in different plant species (Souza et al. 2017). In large areas of invasive species infestations, like natural forest settings, mechanical control can be ineffective or unfeasible and chemical control can be impossible for reasons of cost or application (Gibson et al. 2014). The development of mycoherbicides may offer an alternative to overcome some of these limitations. Similar to mycopesticides, mycoherbicides offer a variation of applications that can aid plant management (Table 1). Their application may reduce the growth of invasive species to allow the growth and competition of native species or target invasive species to cause mortality (Souza et al. 2017). While mycoherbicides can be host-specific, the application of mycoherbicides with broader host ranges can be more beneficial for the preservation and restoration of natural environments infested with invasive species (Barton et al. 2014). Secondary or bioactive metabolites derived from phytotoxic fungi can also be identified and used as natural herbicides (Evidente et al. 2008a,b; Souza et al. 2017). Harnessing the qualities of phytotoxic fungi may hold the key to the limitations and issues associated with chemical herbicides.

Case studies using mycoherbicides

The fungus *Sclerotium rolfsii* is a broad-host-range plant pathogen that infects over 500 plant species and causes various types of infections (Dwivedi and Prasad 2016; Gibson et al. 2014). Gibson et al. (2014) isolated a strain of *S. rolfsii* from a New York state park where invasive pale swallowwort (PSW) was found. PSW is an exotic swallowwort species from Europe that poses a serious threat to eastern North America's natural and rural environments, some of which are home to native endangered species and dependent wildlife (Gibson et al. 2014; Weston et al. 2005). *S. rolfsii* displayed mortality in PSW and black swallowwort (BSW) seedlings in previous laboratory tests done in an earlier study by Gibson et al. (2012). The area in which this strain of *S. rolfsii* was collected did not display negative effects on the surrounding native species but did show signs of infection on the present PSW (Gibson et al. 2014). Gibson et al. (2014) tested this strain to observe if it was a swallowwort specific pathogen or if it had other target hosts. Their study found that while some native swallowwort-related species had 100% mortality in 5 weeks in all species, PSW and BSW had 67%-100% mortality in 5 weeks (Gibson et al. 2014). Some habitat-associated species, primarily dicots, were also affected by 75%-100% mortality in their respective species, but generally constituted lower amounts of plant cover in the native environment (Gibson et al. 2014). However, the habitat associated with monocot species and the predominant grass, *Schizachyrium scoparium*, was mildly to non-affected by the tested strain of *S. rolfsii* (Gibson et al. 2014). They also returned to the collection site of the strain and observed a reduction in PSW growth, which in turn resulted in the establishment of a native species (Gibson et al. 2014). Overall, their results showed targets other than swallowworts but a potential for *S. rolfsii* as an invasive swallowwort mycoherbicide.

Interest in mycoherbicides has extended beyond the direct application of fungal bodies to target plants. Bioactive metabolites derived from phytotoxic fungi are a potential source of natural herbicides (Evidente et al. 2008b). *Cirsium arvense* (L.) Scop., also known as Canada, California, or creeping thistle, is an invasive species that causes widespread damage in pastoral, rangeland, and crop lands (Bourdôt et al. 2006; Evidente et al. 2008b). *Sclerotinia sclerotiorum* (Lib.) de Bary was initially investigated as a potential mycoherbicide for *C. arvense* (Bourdôt et al. 2006). This known plant pathogen is believed to be a safe application for *C. arvense* because of its safe application to other grasses and clover species in pasturelands (Hurrell and Bourdôt 1993), and its relative containability (De Jong et al. 2002) poses no threat to adjacent croplands. However, after studying its annual effects with single and multiple applications on *C. arvense*, *S. sclerotiorum* was shown to be the most effective within the first year of its application and did not compound its effects with annual reapplications (Bourdôt et al. 2006). With no other means of biocontrol, Evidente et al. (2008b) began investigating the bioactive metabolites of *Phyllosticta cirsii* as a possible source of natural herbicides. A previous study by Evidente et al. (2008a) determined four bioactive metabolites from *Phyllosticta* which were identified as phytotoxic. Their second study on *P. cirsii* revealed two additional phytotoxic compounds, which were tested to observe their effects on *C. arvense* (Evidente et al. 2008b). Of these two compounds, phyllostoxin was determined to cause necrosis and display no antimicrobial or zootoxic traits, making it a potential candidate as a natural herbicide (Evidente et al. 2008b). This example displays multiple applications that fungi offer. In the case of insufficient results of direct application, another fungal application offers a more lethal solution to this problematic weed (Bourdôt et al. 2006; Evidente et al. 2008b).

With a large diversity of fungi available and their diverse roles in the environment, mycoherbicides can also harness the application of more than one fungal species (Mitchell et al. 2008). And as a step further, mycoherbicides can also be a beneficial aid to chemical herbicides (Mitchell et al. 2008). Mitchell et al. (2008) wanted to determine the effect of combining two fungal pathogens to manage *Sorghum bicolor* (L.) Moench. *ssp. drummondii* (Nees ex Steud.) de Wet ex Davidse, also known as shattercane. They also wanted to observe the effects of these fungi in combination with the generally effective chemical herbicide glyphosate (Mitchell et al. 2008). Their results showed that two fungal species, *Colletotrichum graminicola* (Ces.) Wils. and *Gloeocercospora sorghi* D. Bain and Edg., were effective in decreasing the percentage of biomass, with an average of approximately 50% (Mitchell et al. 2008). They also found that sublethal levels of glyphosate applied 1 or 3 days prior to either fungal species resulted in 100% biomass loss, which was approximately double the percent biomass loss of unaided glyphosate application (Mitchell et al. 2008). A possible alternative to the insufficient management results of a single mycoherbicide or generic solo chemical herbicide may be the introduction of a second fungal pathogen to either application. As Mitchell et al. (2008) indicated by their results, this may be a more effective IPM method.

As previously mentioned, plants have varying relationships with fungi in their environment (Boddy 2016a, 2016b; Watkinson 2016). Although fungi can be symbiotic to plants, they can also be a very potent tool for their management (Evidente et al. 2008b; Gibson et al. 2014; Mitchell et al. 2008). Their phytotoxic compounds and parasitic forms are both sustainable options for invasive plant management. Although perhaps not ideal to still rely on chemical herbicides, Mitchell et al. (2008) determined the effectiveness of mycoherbicides in collusion with chemical herbicides to manage a difficult invasive species. While there is no apparent universal mycoherbicide currently available, the applications discussed here open the door for determining effective mycoherbicide development.

Use of fungi in forest restoration

In recent decades, global initiatives have promoted ecological restoration and sustainability methods (Asmelash et al. 2016). Degraded lands, lands monopolized by invasive plants, and post catastrophic wildfire conditions are common problems forest managers currently face (Asmelash et al. 2016; Policelli et al. 2020). Asmelash et al. (2016) proposed a possible reason for the failure of restoration efforts owing to the limited attention given to fungi. Incorporating the use of AMF and EMF as restoration tools could lead to future restoration initiatives that surpass past failures.

Degraded lands

Degraded lands are not sternly defined, but can be encompassed in the classification of land that cannot recover from disturbance on its own, resulting in the loss of ecosystem function and productivity (Bai et al. 2008). Under such conditions, plant establishment and success can be heavily stunted. Remnants of heavy metals from mining, soil erosion, and the stripping of land from clear-cutting are all examples of degraded lands (Asmelash et al. 2016; Policelli et al. 2020). Asmelash et al. (2016) compiled results from multiple meta-analyses and found strong support for the use of AMF to increase soil attributes, seedling/shrub establishment and survival, and plant community succession. Policelli et al. (2020) describes the benefits of EMF on eroded soils by promoting the microbial community and improving soil conditions. AMF also play a pivotal role in nutrient cycling and in reducing nutrient leaching (Bender et al. 2015). Depending on the condition of the soil, EMF and AMF can both have a heavy influence on the success of restoration.

Mining operations can leave heavy metals in the soil, which can cause heavy metal toxicity in the resident plants (Policelli et al. 2020). Some EMF and AMF species have been shown to promote host plant success under these conditions in multiple ways (Fernandes et al. 2021; Policelli et al. 2020; see also Figure 2). Depending on the EMF species, high amounts of mycelia and fungal structures around roots create physical barriers between heavy metals and their plant symbionts (Denny and Wilkins 1987; Turnau et al. 1996; Policelli et al. 2020). Another mechanism in which EMF defend plants from heavy metals is by uptaking the metals in their fruiting bodies and in some species, by making these compounds bioavailable (Luo et al. 2014; Leyval et al. 1997; Policelli et al. 2020). While all of these protective mechanisms of EMF are species dependent, EMF inoculation generally promotes survival and occasionally growth in their respective plant symbionts (Denny and Wilkins 1987; Fernandes et al. 2021; Turnau et al. 1996; Sousa et al. 2012).

Clear cutting is the removal of an entire stand, typically used for timber harvesting. This level of disturbance lowers carbon sources from plants and can physically and chemically alter the soil, as well as soil processes, which collectively reshapes the EMF community (Jones et al., 2003). Non-EMF associated plants may also colonize land after a clearcut making EMF plant regeneration difficult (Jones et al. 2003). Retention forestry (Tomao et al. 2020) or living root inoculum (Jones et al. 2003) and soil transplants from mature forests (Amaranthus and Perry 1987) are methods that can be used to minimize this damage to the EMF community and promote seedling establishment and growth after a clearcut (Figure 2).

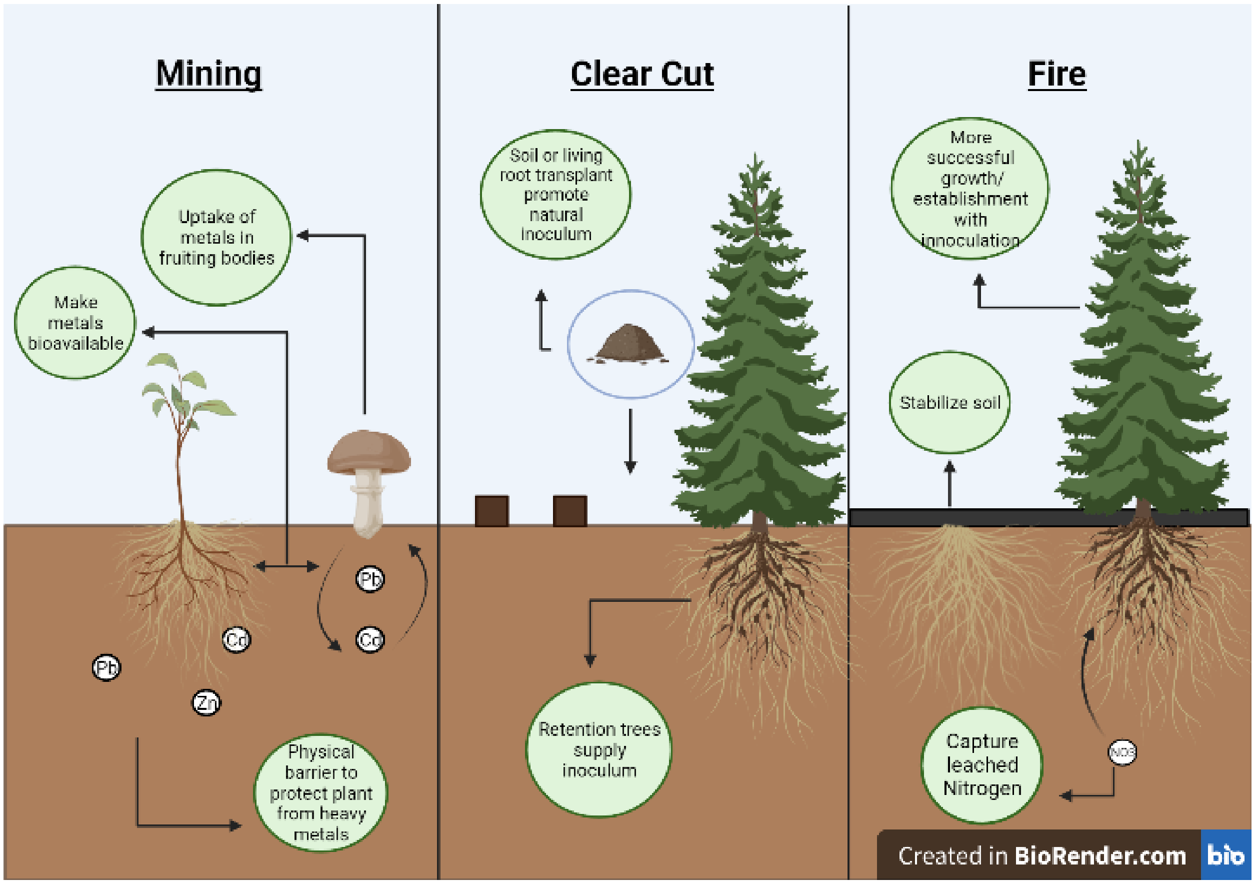

Figure 2. Roles of fungi in restoration after mining, clear-cut, or fire. Created by KP.

Invasive plants

Invasive plants can be problematic in restoration efforts because of their quick establishment and versatility in the environment (Jose et al. 2013). Invasive plants pose a serious threat to biodiversity and are capable of disrupting ecosystem processes (Jose et al. 2013). Although the previous section on mycoherbicides discussed using fungi as a control method for invasive plants, this section will discuss how lands degraded by invasive plants can also be restored with fungal application. How can managers prevent quick and versatile invasives from moving in and colonizing vulnerable land? Some studies indicate that fungal communities may be the key to doing so. Native and healthy AMF and EMF communities can prevent invasive plant invasions (Asmelash et al. 2016; Policelli et al. 2020; see also Figure 3). One study done by Janos et al. (2013) illustrates this theory between a rainforest and savannah boundary. After fire, a plant species from the savannah ecosystem would invade into the rainforest boundary (Janos et al. 2013). Their study determined that healthy AMF relationships helped the native rainforest plants outcompete the savannah invaders (Janos et al. 2013). While the role of fire in this scenario is still a bit ambiguous, it is likely the destruction of the AMF community by fire played a role in the ability of the savannah plants to invade the rainforest boundary (Janos et al. 2013). Policelli et al. (2020) also supports this method with EMF being used in new plantations to prevent invasive pine establishments. However, avoidance or prevention are not always possible.

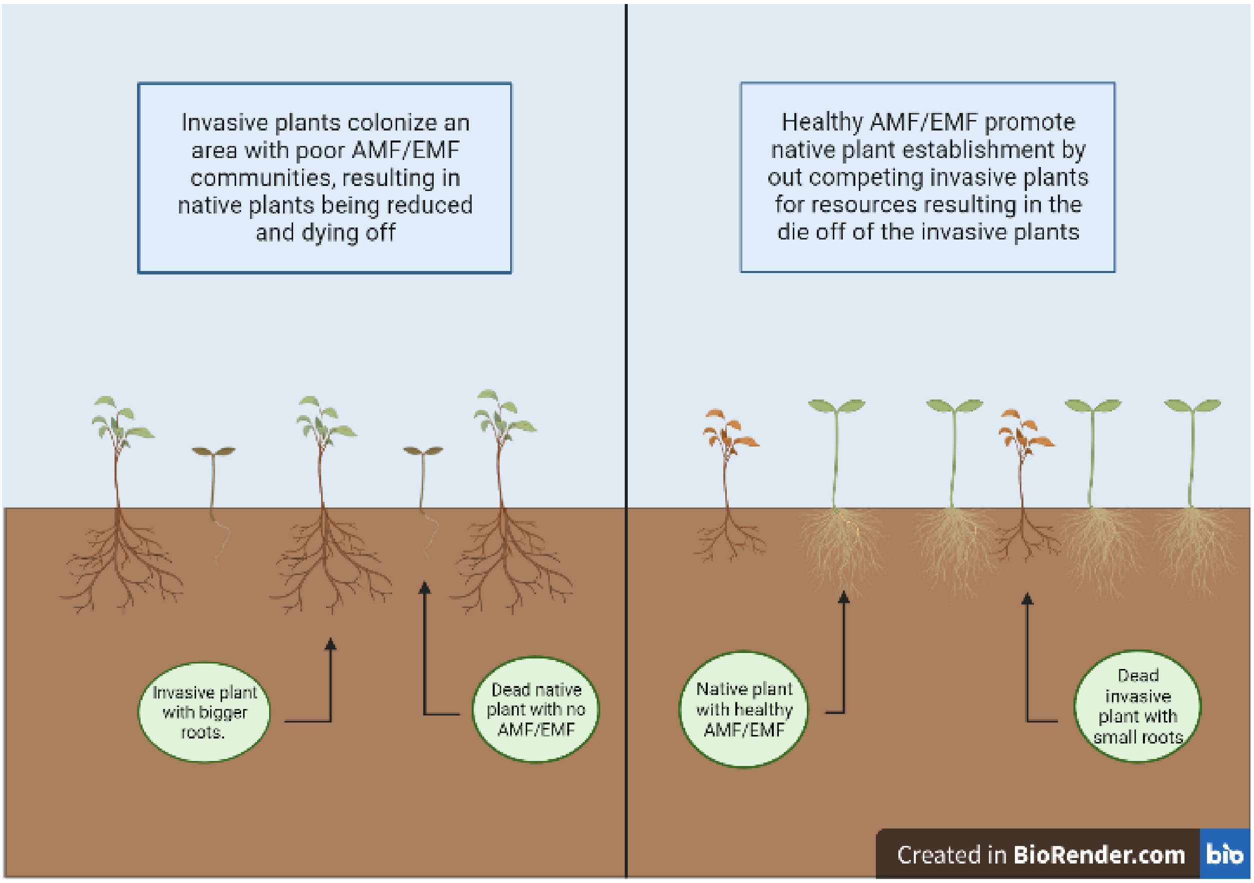

Figure 3. Mycorrhizal fungi aiding native plants to out compete invasive plants. Created by KP.

Policelli et al. (2020) reports that EMF are not currently used to actively manage invaded ecosystems; however their ability to do so is emerging as an option. EMF inoculation has displayed success in promoting native plant establishment in restoration efforts (Amaranthus and Perry 1987; Denny and Wilkins 1987; Fernandes et al. 2021; Policelli et al. 2020; Turnau et al. 1996; Sousa et al. 2012). However, current applications of EMF for invasive plant restoration require the removal of invasive plants prior to implementation (Policelli et al. 2020). Overall, the underground mechanisms of invasive plant management may be a more successful alternative than above-ground methods (Asmelash et al. 2016; Janos et al. 2013; Policelli et al. 2020).

Fire

Fire suppression has led to conditions conducive for catastrophic wildfires (Hart et al. 2018) and reducing the likelihood of high-severity wildfires through fuel reduction treatments is a common management goal (Hart et al. 2018). But forest management often treats post-catastrophic fires. High-severity fires or fires that are not characteristic of an environment can leave restoration efforts with little to go on. However, the remaining fungi and promoting endophytic fungi may be the answers to these post-fire challenges (Figure 2).

Some species of EMF (Glassman et al. 2016) and saprotrophic fungi (Filialuna and Cripps 2021) are fire-adapted depending on wildfire characteristics. One study done by Owen et al. (2019) examined the effects of burn classes on fungal community composition and EMF colonization of naturally regenerating ponderosa pine seedlings 13 years post-fire. High-severity burns favor saprotrophic species to EMF, displaying an overall shift in sporocarp functional groups (Owen et al. 2019). This overall shift to saprotrophic fungal communities in the high-severity burn sites is likely attributable to the fire tolerance of saprotrophic fungi compared to the more susceptible EMF species (Owen et al. 2019). Post-fire saprotrophic fungi lay the groundwork for plant colonization by stabilizing soil and restoring nutrients leached from the burn (Claridge et al. 2009; Filialuna and Cripps 2021).

Theoretically, EMF will passively reestablish after a wildfire if spores or mycelium remain in the soil or spores are available for dispersal near the burn (Glassman et al. 2016). As fungi are responsible for many soil functions, it is not surprising that they would begin the work of restoration post fire. In the study by Owen et al. (2019), ponderosa pine seedlings were also naturally regenerated on the site, and EMF colonization was analyzed to determine the effects of the burn classes. The burn classes, unburned and moderate, showed a similar trend in EMF colonization and species richness, except for the high-severity burn sites, which had lower abundance and different community compositions (Owen et al. 2019). These drastic shifts and unavailability of EMF species for seedling colonization could stunt or even dramatically alter the regeneration of high-severity burn areas. EMF inoculation post-fire has shown success in promoting plant colonization and/or growth (Sousa et al. 2011; Martínez de Aragón et al. 2012). Therefore, in instances such as high severity fires, it may be necessary to inoculate soil to encourage and progress plant colonization (Policelli et al. 2020).

Carbon sequestration

Storing carbon is at the forefront of combating climate-change initiatives. Terrestrial carbon stores, with soils being the largest, can hold exponential amounts of carbon and can even store it for hundreds of years (Hannula and Morriën 2022). This method of sequestering carbon in forests and other soils has been recognized as an option for mitigating climate change (Zhu and Miller 2003). The mechanisms by which carbon is stored in soils involve plants and microbial communities. While other microbes are involved in carbon sequestration, this section will only focus on the role of fungi.

Both AMF and EMF have been observed to play a role in carbon cycling in soils (Asmelash et al. 2016; Averill and Hawkes 2016; Clemmensen et al. 2013; Hannula and Morriën 2022; Zhu and Miller 2003). Endophytic fungi can promote the primary productivity of their plant hosts and macroaggregate soil to trap carbon, store carbon in their living and dead hyphal cells, and stimulate changes in the microbial community to promote carbon cycling (Asmelash et al. 2016; Averill and Hawkes 2016; Clemmensen et al. 2013; Hannula and Morriën 2022; Zhu and Miller 2003; see also Figure 4). Fungi, in general, have higher carbon use efficiency compared to soil bacteria (Allison et al. 2005; Hannula and Morriën 2022; Malik et al. 2016). With varying amounts of carbon allocated between AMF and EMF (Yin et al. 2014), EMF are the more contributing mycorrhizal associate, with their plant host's allocating 20% of their photosynthate to them (Watkinson 2016). Saprotrophic fungi and some endophytic fungi also capture carbon through decomposition of plant material in the litter layer (Averill and Hawkes 2016; Clemmensen et al. 2013; Hannula and Morriën 2022; see also Figure 4). Necromass plays an important role in carbon sequestration in soil (Hannula and Morriën 2022). EMF and saprotrophic fungi have a lower turnover rate than AMF, which is more similar to the higher turnover rate of bacteria (Anthony et al. 2020). Although the living mechanisms of these fungi play multiple roles in carbon sequestration, their necromass accounts for the highest carbon stock compared to other soil microbes and can store carbon in deeper soil layers (Clemmensen et al. 2013; Hannula and Morriën 2022).

While our understanding of the role of fungi in carbon sequestration illustrates their benefits, what does this mean for their application in management? Fungi benefit from global carbon initiatives through their natural processes. To promote this carbon storage mechanism, forest fungi must be promoted. For restoration or healthy forest goals, selecting plants with diverse fungal relationships will promote healthy fungal communities. If possible, limiting soil disturbance would also maintain fungal carbon stocks below ground so as to not damage the necromass in deeper soil layers. Finally, understanding the environmental conditions that sustain healthy fungal communities and creating future models for changes in these conditions due to climate change, will provide managers with tools to boost fungal activity and carbon stores (Clemmensen et al. 2013).

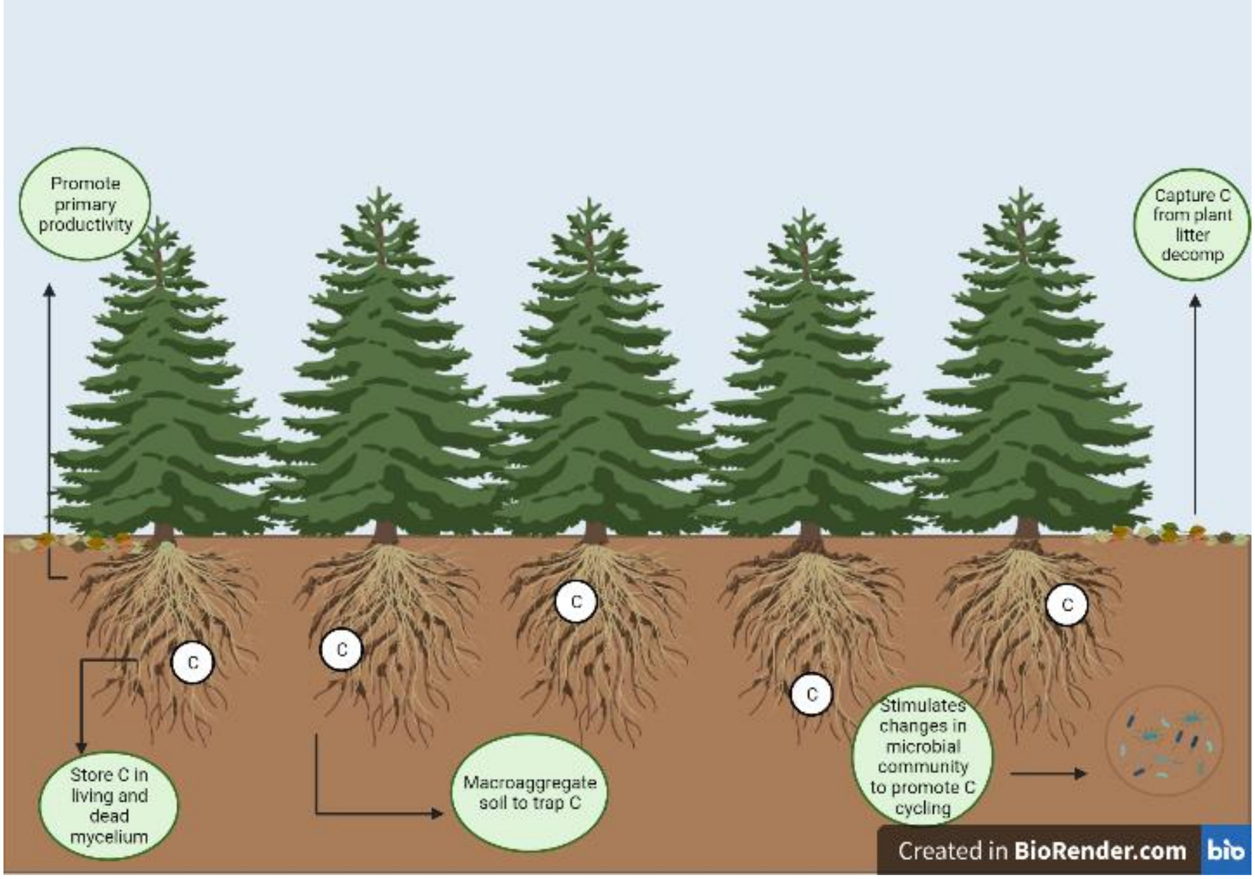

Figure 4. Multifunctional role of fungi in carbon sequestration. C = carbon. Created by KP.

Limitations of the use of fungi

Many studies have demonstrated the powerful contribution of fungi in forest management. However, more research is needed to fully understand and utilize fungi in various ways. As fungi are complex organisms, their physiological delicacy limits our ability to harness their max utility. Therefore, each application of fungi for forest management comes with limitations (Table 2). If a fungus is identified as an efficient and effective management tool, it is not guaranteed that science will be able to identify it at the species level for replication later (Souza et al. 2017). Mass production may not be possible in some instances (Asmelash et al. 2016) and inoculation techniques may not be feasible when a species is not established through spores (Policelli et al. 2020). Lab-tested species or species with idyllic characteristics may not survive in real-world conditions (Policelli et al. 2020) or they may not have long-term survival abilities in general (Gibson et al. 2014). A mycoherbicide can be effective in causing mortality of the target, but may not have an infectivity threshold to make an efficient tool (Bourdôt et al. 2006). Fungal treatments are not site-effect-free; for example, a mycopesticide can have undesirable and damaging effects on natural predators, even though they have desired effects on the target species (Poveda 2021). It is of utmost importance, as science and management move forward, to consider the side effects of fungal application.

Table 2. Forest management applications using fungi with corresponding limitations.

Treatment/forest condition	**Application**	**Limitation**
Mycopesticides	Attract natural enemies, parasitism of microorganism symbiont, plant-symbiont defenses, antifeedant compounds, secondary/repellant metabolites, parasitism	Ability to identify species level of successful EPF, replication/mass production, non-sporulating inoculation, ability to survive in environmental conditions/long term survival, non-targeted effects to other insects
Mycoherbicides	Parasitism, combination application, bioactive metabolites	Infectivity threshold, Ability to identify species level of successful EPF, replication/mass production, non-sporulating inoculation, ability to survive in environmental conditions/long term survival
Degraded land restoration: mining	Promote healthy soil fungi, inoculation	Inoculation with non native fungi may result in adverse effects to environment
Degraded land restoration: clear cut	Retention forestry, mature forest soil transplants, living root transplants	Inoculation with non native fungi may result in adverse effects to environment
Degraded land restoration: fire	Promote healthy soil fungi, inoculation	Inoculation with non native fungi may result in adverse effects to environment
Degraded land restoration: invasive plants	Promote healthy soil fungi, inoculation	Inoculation with non native fungi may result in adverse effects to environment
Carbon sequestration	Promote healthy soil fungi, reduce soil disturbance	Unknown or novel climatic conditions may hinder carbon storage processes in fungal communities

Conclusion and recommendations

In summary, fungi offer sustainable tools for forest management, but as discussed in the previous section, there are still limitations and gaps in our knowledge that need to be addressed (Table 2). As global forests face drastic climatic changes, it is essential to prioritize conservation and sustainability in forest management practices.

Despite the potential benefits of fungi, research into their inclusion in forest management has been lacking. In addition to the examples discussed here, using fungi as forest management tools has many areas that remain to be explored more in depth. Less practiced but potentially growing applications of fungi as agents of fuel-reducing treatments, mycofungicides, and as bioindicators of forest health are also on the horizon. Fruiting bodies or mushrooms of fungi are also an economically valuable forest product that can assist in management objectives (Martínez de Aragón et al. 2012). The more fungi are understood, the more possibilities they hold in managing global forests. Future research should focus on identifying productive fungal species for management objectives, as well as replicating and producing them on a large scale. Additionally, more research is needed to understand the potential side effects of using fungi before widespread application.

To implement these methods in mainstream forest management, collaboration between researchers and managers is essential. By working together, we can bridge the gap between what we know fungi offer and how we can apply them to our forests. This collaboration can help ensure that forest management practices are sustainable and effective, promoting the long-term health and productivity of forest ecosystems.

In conclusion, fungi represent a promising area of research and practice for forest management. With continued research and collaboration, we can harness the potential of fungi to promote ecological sustainability and enhance the resilience of forest ecosystems in the face of ongoing global change.

Personal ethics statement

Respect for nature and the responsibility to uphold its wellbeing is at the foundation of my personal ethics. Forest management must accommodate the services human populations rely on as well as the health and productivity of the land. These two objectives can conflict in various circumstances and a need for sustainable solutions are at the forefront of our forest's futures. The urgent necessity of sustainable forest management practices is what drives my dedication to the field. Economic, political, and cultural services from forests are threatened by climate change. My recommendations for using fungi in forest management are centered around a sustainable and conservation based method of managing future forests so that human life may continue to rely on these services.

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