Impacts of Forest Management on Beneficial Fungi Within the Intermountain West

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Abstract

Forest disturbance and management practices can influence fungal diversity and community composition. In forest management, fungi have traditionally been viewed as undesirable and pathogenic. However, today we realize that many beneficial fungi are crucial to our forest's health. Existing research and published literature show the importance of fungal diversity and the need to develop novel management practices that consider fungal communities. These fungal communities are imperative to the success of our forests in the face of climate change. Managers will need to adapt and work amid fungal communities for our forests to remain healthy and robust. Management practices that promote fungal diversity may be more effective in addressing issues related to climate change than traditional management. When making forest management decisions, considering fungal communities can help promote resilient forests.

1. Introduction

The topics covered in this introduction include a background on fungi and their crucial roles in our natural environments. Before digging in and explaining the importance of fungi, it would be beneficial first to define some terms used in this review. Throughout this review, the term heterotroph will be used as fungi and humans alike are part of this biological group. A heterotroph is an organism that cannot produce its food. While all fungi are heterotrophs, many fungi are further defined as saprotrophs. Saprotrophic fungi derive their nutrition from decaying or dead organic matter. Fungi, along with bacteria, are responsible for most of the decomposition that happens on our planet. Their role as decomposers makes them an essential part of ecological systems, playing important roles in carbon, nutrient, and water cycles. While traditionally, fungi have been primarily thought of as decomposers and pathogenic pests, not all fungi are destructive. Recently, beneficial mycorrhizal fungi have warranted more attention from researchers, and, thus, their importance and value are starting to be recognized.

Mycorrhizal fungi are fungi that exist in soil and live in symbiosis with plants and trees. These fungi live on and in plant roots and help supply plants with water and essential nutrients such as phosphorus and iron. In return, plants provide fungi with carbohydrates that they have sequestered through photosynthesis. This exchange is vital because heterotrophic fungi cannot produce these sugars on their own. These mutualistic relationships are so beneficial that they can be found in approximately 80% of plants (Barman et al., 2016). The mycelial network formed by these soil-dwelling fungi also serves as a communication system

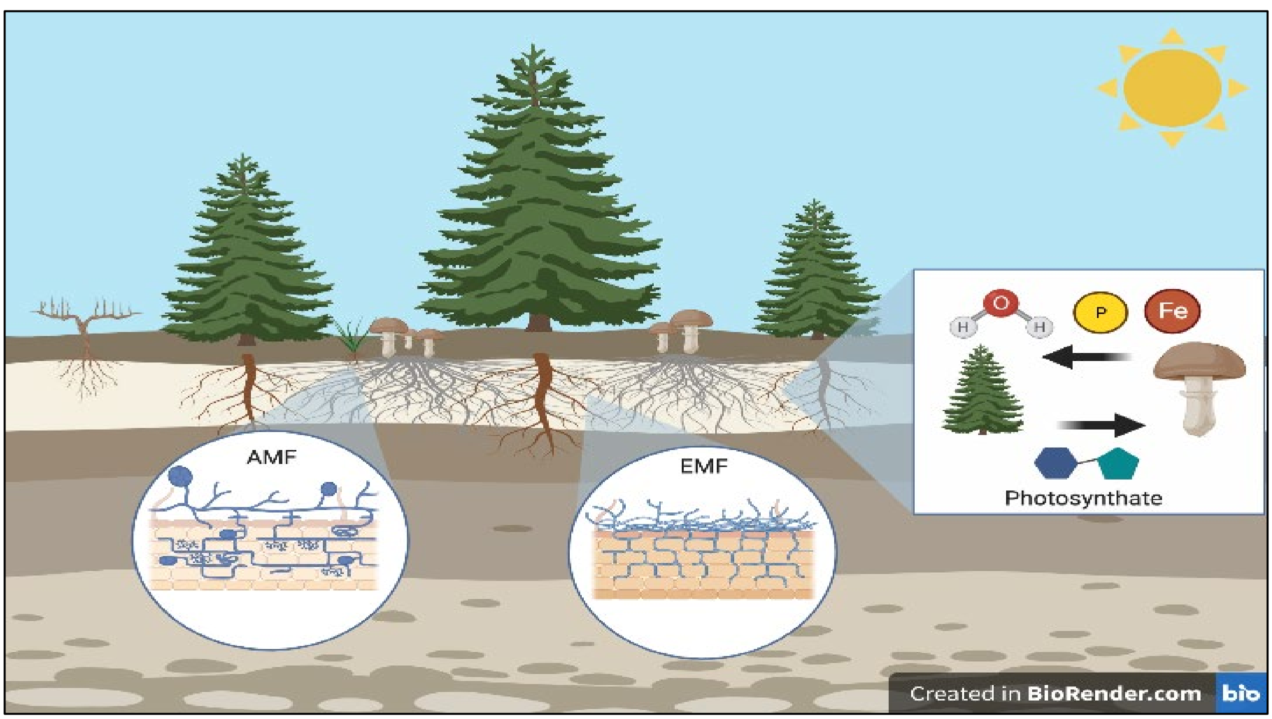

Figure 1. Mycorrhizal network in the soil allows for the exchange of water and nutrients between fungi and plants.

between plants where water, nutrient, and even distress signals can be shared (Figure 1)(Gorzelak et al., 2015).

Two influential groups of mycorrhizae are ectomycorrhizal fungi and arbuscular mycorrhizal fungi. Ectomycorrhizal fungi form a layer on the outside of root tips and benefit roots by protecting them from pathogens (Branzanti et al., 1999), as well as providing water and nutrients. Arbuscular mycorrhizal fungi penetrate the root and form structures called arbuscules. These arbuscules are where the exchange of water and nutrients takes place between the host and fungi. In this paper, these fungi are referred to as AM for arbuscular mycorrhiza and EM for ectomycorrhiza.

While arbuscular mycorrhizal fungi were potentially first described in the mid-1800s, the study and understanding of mycorrhizal fungi is still new and developing (Koide et al., 2004). The lack of knowledge regarding mycorrhizal fungi is genuinely remarkable. We now know that mycorrhizal fungi have relationships with almost all plant families and play a crucial role in drought tolerance (Wu et al., 2017). Mycorrhizal fungi can also benefit plants by making them more resilient and less susceptible to insects and disease. These benefits show the importance of studying these organisms and their unique relationships with their host plants, and their impact on our forested ecosystems. Fungi play significant roles in our forests and ecosystems, and their consideration in management strategies is key to healthy forests.

2. Literature Review and Interpretation

We selected scientific studies that focused on the Intermountain West region of the United States and described the impacts of disturbance and silvicultural treatments on fungal communities. Relevant publications were found using online databases and through analysis of printed literature. For the purposes of this paper, the Intermountain West region is defined as the geographical region located between the Sierra Nevada and Cascade mountain ranges in the west, while the Rockies define the east boundary. Information about forest management and fungi from outside the Intermountain West was added as needed to fill some information gaps.

2.1 Management Related Disturbance

Researchers are observing how management-related disturbances impact fungal communities, their composition, and distribution. This research is key to the ethical and responsible management of our forests and their fungal communities. Recent research has investigated the differences in soil fungal assemblages in managed and unmanaged forests. Kujawska et al. (2021) found that both managed and unmanaged forests upheld fungal diversity; however, management strategy influenced the species composition. After ceasing management, the return of EM fungal composition to the pre-management communities can take upwards of ninety years. This section will discuss how silvicultural practices such as prescribed burning, thinning, and pile burning influence fungal communities. Knowledge of how management practices affect fungal communities is essential to sustainable forest management.

Prescribed Burning

Prescribed burning is a standard silvicultural treatment in the Intermountain West region, where it is used to mitigate wildfire risk and dispose of debris after thinning. Prescribed fire has been shown to affect soil fungal communities. For example, a strong decrease in soil fungal diversity and evenness was observed after prescribed burns (Reazin et al., 2016). Through DNA extraction of soil samples, the authors found that high soil temperatures resulted in the direct mortality of some soil fungi. The most prevalent effects were seen in high severity treatments where the logs were stacked parallel, and ground contact was promoted. The low severity treatment consisted of broadcast burning and yielded similar but less extreme results. The shift in community diversity seemed to be driven by the success of a few fire-loving fungal species.

Korb et al. (2003) investigated vegetation type and soil on plots subjected to three different silviculture treatments of the ponderosa pine (*Pinus ponderosa*) forests of northern Arizona. The treatments included thinning, thinning and prescribed burning, and a no thinning or burning control. They found a positive correlation between grass cover and AM abundance. Both treatments seemed to have a positive effect on AM fungi and a neutral effect on EM fungi compared to the control plots. It was also shown that AM density positively correlated with understory species richness and negatively correlated with tree canopy and litter cover.

The high heat from prescribed burning in stands with high fuel loads can alter fungal communities by selecting for pyrophytic species. Fungal communities can also be influenced by shifts in vegetation populations that occurred from fire. These relationships show how prescribed burning can influence fungal richness in these communities.

Pile Burning

Pile burning is commonly used in the Intermountain West to remove woody debris after thinning treatments. Reazin et al. (2016) investigated how the severity of fire influences fungal community composition in ponderosa pine (*Pinus ponderosa*) forests. In the high severity treatment, logs were piled before burning, similar to a pile used to burn slash. These large piles of large logs burned at very high heat because they were assembled to maximize contact with the ground. This treatment significantly decreased species diversity and distribution, demonstrating how high soil temperatures associated with these burn piles can hinder fungal communities. The authors also found a shift in the dominant phylum of fungi in the soil, from Basidiomycota to Ascomycota. These results show how high-intensity pile burning could alter fungal richness and species composition.

Haskins et al. (2004) studied the effects of pile burning on fungal and vegetation communities in pinyon-juniper woodland of northern Arizona. Results indicate that slash pile burning decreased understory plant diversity and quadrupled the number of exotic plants in burned transects. These exotic plants had 50% greater AM colonization than native plants suggesting that AM populations were not impeded by the fire. Further investigation has shown how pile burning hindered the growth of native species squirrel tail (*Elymus elymoides*) and favored the invasive species cheatgrass (*Bromus tectorum*) (Owen et al., 2013). Invasive species have been shown to produce soil conditions, including fungal communities, that favor their own growth over other species. These discoveries show that pile burning should not be a preferred method to dispose of logging debris and can be destructive to soil and its biome in ponderosa pine and pinyon-juniper forests. (Esquilín et al. 2007, Haskins et al. 2004).

Thinning

Thinning is a common practice used by silviculturists to reduce fuel loads and increase the resilience of forests to biotic and abiotic stressors. Thinning treatments have been shown to influence the abundance and diversity of fungal communities. Overby et al. (2015) showed that thinning altered the community composition of both vegetation and AM fungi. The thinning treatments of Taylor Woods have been in place for over forty years and replicated stand densities similar to pre-Euro-American settlement. Their results indicate that the creation of openings in the canopy supported more native AM-associated plant species and was advantageous to AM abundance and diversity.

Fahey et al. (2012) found that AM colonization of giant sequoia (*Sequoiadendron giganteum*) roots was linked to plant-assimilated carbon availability. Thinning treatments designed to imitate artificial canopy gaps were shown to increase the amount of carbon assimilated by individual saplings. The increased carbon availability to individual sequoia saplings not only increased AM colonization but also promoted sapling growth. These results illustrate how the creation of gaps and thus altered carbon availability can increase sapling growth by promoting AM colonization.

While AM abundance is influenced by host plant availability and health, some research shows how different stand structure attributes influence EM communities. In a review by Tomao et al. (2020), uneven-aged stands were shown to promote fungal diversity. Smith et al. (2002) observed similar trends in Douglas-fir (*Pseudotsuga menziesii*) stands in Oregon, where 36% of EM species were unique to a specific age class of Douglas-fir, including fifty species unique to old growth. Age classes compared in the study consisted of young with closed canopy (30-35 years), rotational age (45-50 years), and old-growth (>400years).

Tomao et al. (2020) conclude that low-intensity treatments like selective cutting promote EM fungal diversity. This information illustrates how maintaining an uneven-aged stand can promote beneficial fungal activity and diversity. Thinning is not only necessary for fuel reductions in some situations but can also be used to encourage fungal diversity. For example, openings can be created to support AM-associated understory species, and selective cutting can be used to promote diverse EM-associated stands. These fungal communities are essential for forest health and resilience.

2.2 Natural Disturbances

Climate change is rapidly altering disturbance regimes and, in turn, altering fungal communities (Turner. 2010). Information on how natural disturbances influence fungal communities is vital for managers to address recovery from them. These fungal communities are important to ecosystem resilience and recovery. Figure 2 illustrates some of the factors influencing mycorrhizal fungi.

Wildfires

With wildfires increasing in frequency and severity across the West (Westerling et al., 2006), it is vital to understand how wildfires affect fungi. High severity wildfires have been shown to alter fungal diversity and composition (Pulido-Chavez et al., 2021). The authors found that EM richness was 43.4% lower in severely burned plots of ponderosa pine than adjacent unburned plots. The severe plots had 100% tree mortality, and eleven years after burning, fungal communities did not recover to undisturbed levels. Furthermore, severely burned plots contained 12.2% fewer saprobic species than the unburned plots. The success of fire-tolerant species of fungi caused the alteration of species composition in EM and saprobic fungi. These outcomes show how severe wildfire can impact fungal communities. As wildfire frequency and severity increase across the Intermountain West, current fungal communities are at risk.

Other Natural Disturbance

Herbivory has been shown to have a significant influence on mycorrhizal fungal communities (Gehring et al. 2002). The authors observed how herbivory by moose and snowshoe hare reduced mycorrhizal colonization of balsam poplar (*Populus balsamifera*) and willow (*Salix spp*.). Although not all mycorrhizal fungal species are equally affected by the grazing of their associated plants, herbivores negatively affect mycorrhizal colonization (Gehring et al., 2002). Because all species are not affected equally, it is vital to keep in mind that other disturbances are likely to impact fungal species differently. These findings are evidence of a need for further research and understanding of how different mycorrhiza species respond to various disturbances.

Other biotic factors impact mycorrhizal communities, such as plant community composition and distribution. Cripps et al. (2005) assessed how mycorrhizal types might differ on different families of plants. They found that species associations between plants and fungi seemed to be relatively consistent among families. They also observed unique species associations between plants and fungi. The patchy distribution of fungal communities showed that the soil biome was not uniform throughout the study site and created a mosaic of different fungal communities (Cripps et al., 2005). This study shows how an ecosystem's mycorrhizal fungal community structure can play a role in the distribution and composition of plant types.

2.3 Climate

Mycorrhizal fungi can play an important role in host plant survival and success (Swaty et al., 2004). Through analysis of tree rings and EM communities, Swaty et al. (2004) demonstrated that mortality rates of adjacent stands of pinyon pine (*Pinus edulis*) were negatively correlated with EM colonization. In addition, the remaining trees in high mortality stands continued to struggle and often succumb to future drought due to EM scarceness. This research underlines the importance of EM colonization and shows how reducing EM colonization can decrease tree performance and longevity.

We are still limited by our understanding of mycorrhizal communities and their interactions; however, recent research shows this field's potential to combat climate change. Gehring et al. (2017) looked at different genotypes of pinyon pine and their associated mycorrhizal communities around Flagstaff, Arizona. Long-term studies in the field, greenhouses, and common gardens revealed that ectomycorrhizal community composition is affected by host plant genetics and that seedlings have a genetic propensity for the EM fungal community composition of their seed source tree. This relationship shows that drought resistance is a heritable trait and, therefore, seed source should be considered for operational plantings. This work shows just how unique the relationships between plants and fungi are and demonstrates the importance of appropriate seed source in plantings.

This research also shows how genotype-specific communities play essential roles in plant performance during climate stress. Taking this into consideration might be more critical now than ever as we try to mitigate climate change. Looking to use these drought-resistant genotypes during reforestation will be central to our forest management success in a future of climate change. Through strategic planting, managers could also potentially plant these drought-resistant genotypes to make forests more robust as our climate becomes warmer and dryer.

Similarities in EM communities between tree species may also be used to avoid deforestation, particularly as climate change may render many species maladapted to their current geographic location. For example, due to climate change, lodgepole pine (*Pinus contorta*) is expected to become maladapted to much of its current range (Coops et al., 2011). Ponderosa pine is associated with a very similar EM community and, therefore, may be successful on these sites, avoiding loss of forest cover and preserving the EM community (Garcia et al., 2016).

2.4 Invasive Plants and Associated Fungi

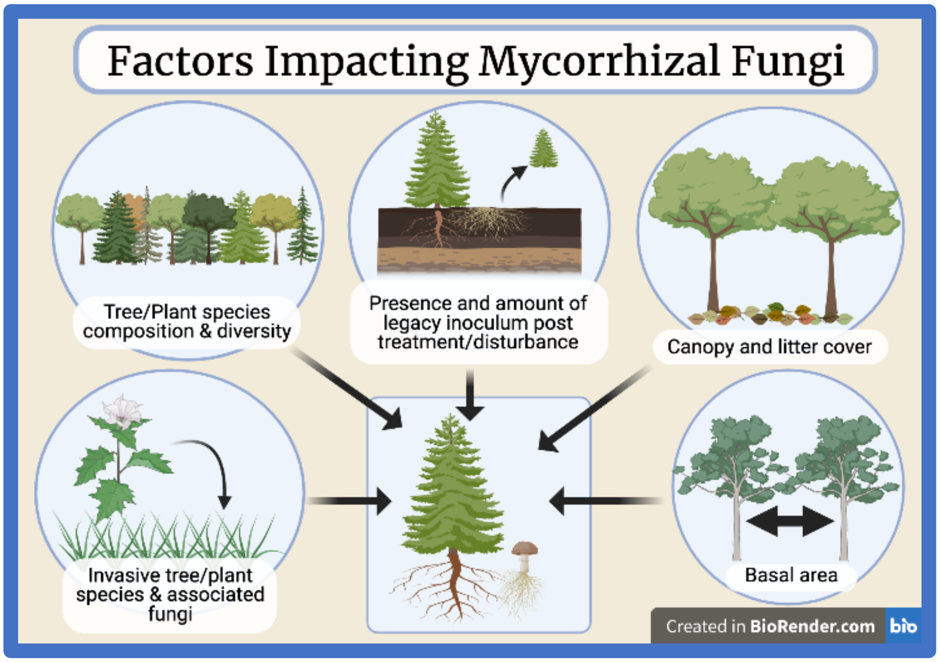

Figure 2. Factors impacting arbuscular and ecto-mycorrhizal fungi

A study by Daniel Mummey et al. (2005) reinforces the idea that the mycorrhizal fungal community plays a role in plant community composition and adds the complexity of an invasive species, *Centaurea maculosa*. Mummey et al. (2005) looked at how neighboring plants impact arbuscular mycorrhizal fungal communities. The evaluation of plots containing the invasive knapweed *C. maculosa* allowed for observing how neighboring plants could impact fungal communities. They found that the presence of the *C. maculosa* altered the genotype of the arbuscular mycorrhizal communities of native *Dactylis glomerata* grass to reflect its own AM communities. The author's observations also found that the fungal symbiont present could be the primary determinate of root colonization. The change in fungal community composition caused by an invasive will influence what fungal symbionts are present and thus, determine root colonization. This observation shows how an invasive species and its management could significantly impact mycorrhizal communities and influence the plant community's structure. Other research shows how once exotic plant communities establish, they often produce soil conditions that favor their growth over native species (Owen et al., 2013)

Hilbig et al. (2015) observed competitive interactions between invasive *Bromus diandrus* and native forbs. Most native forbs had either positive or neutral feedback to introduced AM inoculum. However, this positive feedback did not seem to be enough to offset the adverse effects of increased intraspecific competition. The effects of intraspecific competition appeared to be stronger than interspecific due to small differences in AM symbiosis. The authors point out that it appeared the positive feedback from inoculation was mainly affected by the balance between the presence of AM fungi and introduced pathogens. Another interesting finding of this study was the presence of oomycetes in invasive AM inoculum from the soil of an abandoned citrus orchard. Oomycetes form a phylum of protists that contains many historically significant plant pathogens. These threats are essential for managers to take into consideration when combating invasive species.

3 Fungal Recovery from Disturbance

Increased drought and altered disturbance regimes impact fungal distribution and species composition. Understanding how fungi recover post-disturbance is critical to forest management. This section investigates how fungi recover from several different types of disturbance and how fungi recover naturally versus assisted recovery.

Natural recovery

Researchers have investigated the natural recovery of mycorrhizal fungi after disturbance to better understand ecosystem recovery. To assess mycorrhizal recovery post-disturbance, Allen et al. (1987) surveyed mines and inactive barrow pits for mycorrhizal fungi in alpine ecosystems of the Beartooth Mountains in Montana. Examination of roots in the disturbed and undisturbed plots allowed for assessing how much of the root system was colonized with mycorrhizal fungi. Counting of spores in the soil allowed for identifying different genera and gave researchers an idea of spore densities. Results indicate that once plants colonize an area, mycorrhizal fungi can establish quickly; however diversity of fungal species is more time-sensitive.

Further research has been done on fungal recovery at a longer temporal scale. Hart et al. (2018) observed EM community recovery 15 years post fuel reduction treatment in the Blue Mountains of Oregon. The soil was monitored on plots that were subjected to thinning, burning, and a dual treatment. The authors confirmed that EM communities are moderately resilient to low severity disturbances and observed minimal long-term effects from the thinning and dual treatments on EM communities. The long-term study points out that future objectives of land managers will include creating stands resistant to the effects of climate change, like drought and increased fire.

Scientists are now looking into how these altered disturbance regimes are impacting fungal communities. One study observed the Pumpkin Fire burn area in northern Arizona thirteen years after burning (Owen et al., 2019). Plots were placed in areas of different burn severities to determine how the fire affected fungal communities. Their results showed the high severity plots, >200m from a live tree had 5-13 times lower sporocarp densities and 4-7 times lower EM species richness. The lack of fungal species richness is concerning, as they are important to ecosystem recovery (Kardol et al., 2010). When combined with the results of other studies, it is clear that severe disturbances can alter EM communities and, in turn, impair ecosystem resilience.

Assisted Recovery

Scientists are exploring if fungal communities can be supplemented through the use of inoculums. These inoculums are fungal spores that can be applied to seedling roots transplanted on restoration and replanting sites. A meta-analysis has been performed to determine AM inoculums' effectiveness and had some very relevant findings about mycorrhizal management (Rúa et al., 2016). The analysis was centered around local adaption, which is the variation of different genotype's success in their natural and foreign environments. This property allowed for the discovery of several realizations about inoculums that have been overlooked. By examining different sympatric (from the same environment) and allopatric (from different environments) combinations of plant, soil, and fungi, the authors revealed that the plant, soil, and fungi's geographical origin is essential to host vitality. The results showed that AM inoculation's effect was most significant when the plant and soil had the same geographic origin. The results indicate the relationship with the soil regulates local adaption of AM relationships. This study's findings show how critical the use of local inoculums is and points out that many restoration efforts use inoculum from producers that do not match the local AM relationships.

Another significant facet of this analysis is consideration of inoculum complexity and its effect on host biomass. The results showed how multiple taxa of fungi are more beneficial than an inoculum containing a single species (Rúa et al., 2016). One of the authors' interesting observations was that inoculums with a single species showed a more significant sympatry effect, which would indicate local adaption. Inoculums containing multiple species, however, can provide a greater benefit to the host in a wider range of environments. When plant and fungi were of the same geographic origin but allopatric to the soil, there was a less positive response by the host plant. The conclusions illustrate how multi-species inoculums are preferential and suggest that fungi adapt to the soil to be less mutualistic with new host plants.

Other research has investigated the conditions that influence inoculum success on restoration sites. Neuenkamp et al. (2019) found inoculums extremely successful, especially on sites with degraded soils that lacked phosphorus. Other factors that influenced inoculum effectiveness were host plant nutrient demand and nutrient use efficiency. This study also shows inoculums work best on plant groups with high nutrient demands like C4-grasses and woody nitrogen fixers. Consequently, the complexity of an inoculum's potential has resulted in the varied success of inoculums.

4 Management implications

With the advancement in the study of forest management impacts on fungal communities come implications for forest management. With altered climate and disturbance regimes, it is more critical than ever for managers to have mycological knowledge and resources. This knowledge will be helpful as managers need to work with fungal communities to ensure healthy forests. Attention to these fungal communities is critical to our forests' success as our climate becomes warmer and drier.

Limitations

One of the significant obstacles to the management of forest fungi is our lack of knowledge about them. Discoveries about these organisms have remained limited due to their obscurity. Fungi are often referred to as the hidden kingdom because they are usually only observed when fruiting, i.e., producing mushrooms. Through advancements in molecular DNA technology, scientists are discovering important information for management. In a study in the Cascade mountains of Oregon, Van Norman et al. (2021) reported that the fungus *Bridgeoporus nobilissimus* was thought to be rare but is not rare at all (Van Norman et al., 2021). The authors found that *B. nobilissimus* seldom produced fruiting bodies and was present in roughly 41% of the mountain range. This study reveals how limited our knowledge is about fungi in our forests, let alone all their complex interactions.

Another impediment to the management of fungi is taxonomic uncertainty. Molina et al. (2011) explain how the abundance of undescribed species and the numerous morphological resemblances of taxa create uncertainty for management. Taxonomic uncertainty coupled with our lack of knowledge has challenged managers. Through further research and improved technology, managers can improve current practices and create novel forest management practices that consider fungal communities.

Opportunities

While thinning is often used to maintain healthy forests, new research shows how we deal with debris post thinning has a significant influence on soil health (Owen et al., 2009). Owen et al. (2009) determined that mastication is a preferred method to deal with debris from thinning treatments. The authors found that two and a half years post-treatment, pinyon-juniper plots treated with masticated wood chips had more plant cover and species richness versus the untreated plots. The southwestern Colorado study also found that the mastication method resulted in improved soil conditions and less invasive species than pile burning.

Paul Stamets explains how not burning woody debris after thinning is beneficial to all fungal species (Stamets. 2005). Stamets suggests that thinning is necessary for the health of forests and mitigating fire danger. He further clarifies that retaining the woody debris on site is vital to returning nutrients to the environment. The residual woody debris can then be disassembled by saprophytic fungi releasing nutrients and invigorating the soil biome. Stamets endorses using oil that contains selected saprophytic fungi spores in the chainsaws used in thinning to accelerate the process. Aside from returning nutrients to the biome and increasing fungal diversity, mulching has other benefits as well. Some other substantial benefits gained through mulching are decreased erosion and higher soil moisture content (Owen et al. 2009, Stamets. 2005). The benefits signify that, when feasible, mastication should be preferred to dispose of woody debris in thinning and logging operations.

A study by Luoma et al. (2013) tested to see the effectiveness of different inoculums used to supplement seedlings on green-tree retention sites in the Umpqua National Forest. By monitoring transplant seedlings, they determined that inoculum had no significant benefit to seedlings. However, the importance of green-tree retention for retention of legacy inoculum of ectomycorrhizal fungi was shown to be very important. This is consistent with the findings of Owen et al. (2019), where a distance greater than 200 yards from a live tree severely decreased EM richness and sporocarp densities. These remaining fungi are essential for the recovery of EM fungi in areas where there have been timber harvests and need to be considered by forest managers.

In a different study, Luoma et al. (2006) explore the effect of distance from retention trees on the EM communities of seedlings. Their findings suggest that a distance >5m from a retention tree will change the EM community structure of seedlings. The results show how imperative proximity to a retention tree is to a seedling. The research further establishes the importance of retention trees to serve as refugia for seedlings to develop EM communities. These fungi will likely be even more important as our climate gets drier; managers will need to ensure a legacy inoculum for seedlings to have the essential fungal community to survive drought.

Suppose we combine this knowledge with the findings from Allen et al. (1987) and Korb et al. (2003), where they found that the establishment of species diversity takes time and a positive correlation between grass cover/species richness and its arbuscular mycorrhiza abundance. It could be assumed that the presence and amount of legacy inoculum on a site would play a role in the trajectory and rate at which a site recovers post-disturbance. This research could also be used by managers when trying to accelerate recovery post-disturbance. Managers could potentially look to establishing diverse native ground cover post-disturbance to promote mycorrhizal fungal diversity.

Even though inoculums were not beneficial in the Luoma et al. (2013) study, inoculums could help sites with little legacy inoculum or highly degraded soils (Neuenkamp et al., 2019). This jumpstart could be particularly helpful when managers want to quickly establish ground cover after severe disturbances. Furthermore, Rúa et al. (2016) showed the intricacy of an inoculum's potential. The authors showed how it was beneficial to use complex local inoculums. These findings suggest that the use of inoculums can be beneficial when used appropriately.

Conclusions

The term mycoforestry has been coined to describe an offshoot of ecoforestry that highlights beneficial fungal roles (Stamets, 2005). The further development of such practices is vital to the health of our forests. These fungal communities are imperative to the success of our forests in the face of climate change. Managers will need to adapt and work with fungal communities for our forests to remain healthy and productive. Healthy and diverse fungal communities promote forests resilient to disturbance and, therefore, need to be considered in management decisions. The significance of managing disturbance-resistant forests is more significant than ever as climate change alters disturbance regimes.

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