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Back to Roots: The Role of Ectomycorrhizal Fungi in Boreal and Temperate Forest Restoration

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Temperate and boreal forests are increasingly suffering from anthropic degradation. Ectomycorrhizal fungi (EMF) are symbionts with most temperate and boreal forest trees, providing their hosts with soil nutrients and water in exchange for plant carbon. This group of fungi is involved in woody plants' survival and growth and helps plants tolerate harsh environmental conditions. Here, we describe the current understanding of how EMF can benefit temperate and boreal forest restoration projects. We review current evidence on promising restoration plans that actively use EMF in sites contaminated with heavy metals, affected by soil erosion, and degraded due to clearcut logging and wildfire. We discuss the potential role of this group of fungi for restoring sites invaded by non-native plant species. Additionally, we explore limitations, knowledge gaps, and possible undesired outcomes of the use of EMF in forest restoration, and we suggest how to further incorporate this fungal group into forest management. We conclude that considering EMF–host interactions could improve the chances of success of future restoration programs in boreal and temperate forests.

Keywords: belowground biota, clearcutting, soil erosion, plant-soil feedbacks, post-fire restoration, mining reclamation, soil management

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INTRODUCTION

Forest ecosystems are undergoing a process of anthropic degradation globally (DeFries et al., 2010). This process is reducing biodiversity and negatively affecting the goods and services they provide (Chazdon, 2008; Aerts and Honnay, 2011). In temperate and boreal forests, most woody plant species are obligate partners with ectomycorrhizal fungi (EMF), which provide nutrients (e.g., nitrogen, N) and water to host trees in exchange for photosynthetically fixed carbon (C) (Smith and Read, 2008). Due to the prevalence of this symbiotic interaction, EMF have a potentially critical role in restoration and management interventions in these ecosystems (Hawkins et al., 2015, **Box 1**). However, their current use in forest restoration and management is limited and their direct manipulation to achieve restoration objectives is even less common (Heneghan et al., 2008).

Several lines of evidence indicate that using mycorrhizal fungi as a tool for restoration can be cost-effective and have long-term results. Anthropic activities can negatively affect the abundance and richness of the EMF community in forest soils due to soil erosion, changes in land use,

BOX 1 | What is forest restoration?
Forest restoration often aims to repair ecosystem functions, re-introduce species of special concern, or return forest ecosystems to specified reference conditions (e.g. a historical state) in terms of specific community structures or other traits. Restoration goals are often pragmatic and set by decision makers and institutions investing in them (Stanturf et al., 2014). Goals are generally influenced by the degree of degradation, regional climate, and interests of local people and stakeholders (Jacobs et al., 2015). It is generally impossible to recreate ecosystem conditions that existed prior to anthropic or natural disturbance because of local extinctions, shifts in climate conditions, or other irreversible changes in conditions. Thus, many restorations focus on restoring specific ecosystem functions, particularly in a context of rapid climate and land use changes (Stanturf et al., 2014).

inorganic toxins, fire, and non-native plant invasions (Pringle et al., 2009; Maltz and Treseder, 2015; Asmelash et al., 2016). Inoculation with specific soil microbes can facilitate the establishment and growth of plant species of interest in degraded ecosystems, while also improving soil quality (Requena et al., 2001; Jeffries et al., 2003; Harris, 2009; Kalucka and Jagodzinski, 2016). For example, inoculation with arbuscular mycorrhizal fungi (AMF) can promote the development of early successional grasses in tallgrass prairies (Smith et al., 1998; Richter and Stutz, 2002) and may help restore focal plant species to degraded soils, such as mining soils (Maltz and Treseder, 2015; Koziol et al., 2018). Additionally, the use of transplanted seedlings with appropriate microbes in their roots, or the use of cover crops associated with mycorrhizal symbionts, can help ensure inoculum availability for later-establishing plant species (Jeffries et al., 2003; Piñeiro et al., 2013). There are some examples in which no effect of mycorrhizal inoculation was detected in field restoration experiments (Teste et al., 2004; White et al., 2008; Sýkorová et al., 2016), yet these constitute a small fraction of the published studies on microbial-assisted restoration.

Ectomycorrhizal fungi interactions with the dominant plant species in forests are better understood and described than those of other soil organisms (Horton and Bruns, 2001; Soudzilovskaia et al., 2019), which makes them particularly promising for use in restoration of specific associated plant species. Moreover, their functional role in ecosystems and their interactions with other plant and soil organisms in forests are becoming clearer (Lilleskov et al., 2002; Phillips et al., 2013; Hewitt et al., 2015; Steidinger et al., 2019), which is particularly important for managers aiming to restore ecosystem functionality (Heneghan et al., 2008). EMF are involved in post fire regeneration, plants' tolerance and absorption of inorganic contaminants, and recovery after plant invasions (Colinas et al., 1994; Baar et al., 1999; Martínez et al., 2012; Sousa et al., 2014; Dickie et al., 2016; Kalucka and Jagodzinski, 2016).

Here, our objective is to gather current evidence on the effectiveness of actively using EMF in temperate and boreal forests restoration programs. We discuss their application in different degraded ecosystems and the possible limitations in their use. Specifically, we ask: Are plant–EMF interactions considered by active restoration plans? Is there evidence that the use of EMF can enhance restoration outcomes? Which are the main disturbances after which EMF restoration have been applied? What are the potential uses of EMF restoration in the future and what are the possible limitations in their use? To answer these questions, we performed a global review of the literature in November 2019, gathering published works addressing the use of EMF for a forest restoration objective. We used Scopus to perform a first search with the terms ectomycorrhiza* AND forest AND restor* in the title, abstract and/or keywords. After generating a list of 101 documents, we complemented that list with the same search in Google Scholar and Web of Science to check for possible missing papers in the Scopus search. We obtained a final list that contained a total of 140 documents. We only considered papers that specifically evaluated the role of EMF in restoration programs performed in temperate and boreal forests and used ectomycorrhizal plant hosts, checked for effective EMF colonization of plants' roots, and considered the use of untreated plants for analyses (e.g., comparing biomass of EMF inoculated vs. non-inoculated plants in the field). We discarded those papers that evaluated only AMF, or addressed the effects of any kind of disturbance on diversity of the EMF community. From the papers obtained, we gathered and summarized information about the study site, the EMF species inoculated and the target host species, if informed.

PROMISING APPLICATIONS OF EMF IN FOREST RESTORATION

Despite its potential as a restoration tool, a relatively low number of studies have directly manipulated the EMF community to meet a restoration goal in temperate or boreal forests (**Table 1**). A total of 13 studies met the criteria used, all of them performed in the Northern Hemisphere. In most of the studies, mining is addressed as the major source of forest degradation, considering heavy metal contamination in the soil and soil erosion. Clearcut logging, other sources of soil erosion and wildfire are the other disturbances addressed. Although a relatively high number of papers addressed the effects of plant invasions on the EMF community, we found no papers directly manipulating the EMF community (native or non-native) to achieve forest restoration in invasion contexts. Most of the studies used EMF-inoculated plants in the nursery prior to assessing their growth and survival in the field, although we found some cases in which direct manipulation in the field was performed in post-mining sites. Restoration, measured in terms of establishment and growth of inoculated (compared to non-inoculated) target plant hosts was generally reported to be successful, although we found some exceptions (**Table 1**).

Heavy Metal Contamination

One type of restoration in which EMF appears to be particularly effective is in restoring forest soils contaminated with heavy metals (**Figure 1A**). While organic contaminants can be degraded, metals generally need to be physically removed or immobilized. Certain fungi and bacteria are able to make metals bioavailable (Krumins et al., 2015). From the 13 papers found, five addressed restoration of contaminated areas after mining, but two of them specifically addressed contamination with heavy

TABLE 1 | Summary of the studies that address the role of ectomycorrhizal fungi in temperate or boreal forest restoration.

Citation	Disturbance type	Location	Type of study	EMF species used	Host species	EMF attributes used to achieve restoration goal
Bauman et al. (2012)	Mining/soil erosion	Ohio, United States	Field experiment	*Scleroderma* sp. *Thelephora* sp. *Pisolithus* sp. (found associated both with *Pinus virginiana* and *Castanea dentata* trees)	*Castanea dentata*	EMF specificity in the association with their plant hosts: shared EMF species between two plant hosts improve the growth and survival of the target plant species near stands of the other host.
Bauman et al. (2013)	Mining/soil erosion	Central Ohio, United States	Inoculation at nursery and subsequent field experiment applying mechanical soil treatments	*Pisolithus tinctorius*	*Castanea dentata*	Rapid root colonization of early successional EMF after mechanical disturbance of soil: soil subsurface methods increase EMF colonization and seedling growth of the target plant species
Caravaca et al. (2002)	Soil erosion	SE Spain	Field experiment	*Pisolithus tinctorius*	*Pinus halepensis*	EMF improvement of soil stability: EMF inoculation on target plant species increases the structural stability of the soil mainly due to a reactivation of microbiological activity
Colinas et al. (1994)	Clearcut	SW Oregon, United States	Soil inoculation in the field	Soil inoculum with multiple EMF species	*Pseudotsuga menziesii*	EMF species tolerance to harsh conditions: Soil transfers from mature adjacent forests facilitates the colonization of certain early successional EMF, favoring a suitable environment for the microorganisms already present in the microsite.
Franco et al. (2014)	Fire	Northern Portugal	Inoculation at nursery and subsequent field experiment	*Hebeloma crustuliniforme* *Laccaria laccata* *Lactarius deliciosus* *Pisolithus tinctorius* *Rhizopogon vulgaris* *Suillus bovinus* *Suillus granulatus*	*Pinus pinaster*	Persistence after field establishment of certain EMF species inoculated in the nursery: EMF inoculation benefit target plant growth, with certain EMF species persisting in the post-fire sites once translocated from nursery.
Martínez et al. (2012)	Fire	NE Spain	Inoculation at nursery and subsequent field experiment	*Tuber melanosporum*	*Quercus ilex*	Potential economic importance and long lasting inoculation effects of some EMF species: Inoculated plant hosts exhibited higher survival rate and greater aerial and root systems than non-inoculated hosts. The inoculated EMF species, with high commercial interest, was not replaced by the local post-fire EMF community in the long term.
Onwuchekwa et al. (2014)	Mining/soil erosion	Alberta, Canada	Inoculation at nursery and subsequent field experiment	*Hebeloma crustuliniforme* *Laccaria bicolor* *Suillus tomentosus*	*Pinus banksiana* *Picea glauca*	EMF capacity to improve salinity resistance and water uptake: Inoculation with certain EMF species increased growth of *P. banksiana* and increased survival of *Picea glauca* planted in oil sands reclamation areas.

(Continued)

TABLE 1 | Continued

Citation	Disturbance type	Location	Type of study	EMF species used	Host species	EMF attributes used to achieve restoration goal
Rincón et al. (2007)	Soil erosion	Madrid, Spain	Inoculation at nursery and subsequent field experiment	*Amanita ovoidea* *Rhizopogon roseolus* *Suillus collinitus*	*Pinus halepensis*	EMF capacity to provide stress tolerance to compatible hosts: Inoculated plant hosts transplanted to the field increase their survival and growth, but the beneficial effect depends on the EMF species inoculated.
Roldán and Albaladejo (1994)	Soil erosion	SE Spain	Inoculation at nursery and subsequent field experiment	*Pisolithus tinctorius* *Rhizopogon roseolus* *Suillus collinitus*	*Pinus halepensis*	Stress tolerance capacity of early successional EMF species: target seedlings inoculated with early successional EMF show beneficial growth and nutrient assimilation responses in the field. Positive response depends on the EMF species inoculated.
Sousa et al. (2011)	Fire	North Portugal – soil from temperate forest	Greenhouse bioassay	*Pisolithus tinctorius* *Rhizopogon roseolus* *Suillus bovinus*	*Pinus pinaster*	EMF species capacity to inoculate seedlings at nursery stage in post-fire soil: Target plant seedlings grow better in burnt soil when inoculated with certain EMF species in the nursery. The beneficial effect depends on the EMF species inoculated.
Sousa et al. (2012)	Heavy metal contamination	North Portugal – soil from temperate forest	Greenhouse bioassay	*Suillus bovinus* *Rhizopogon roseolus*	*Pinus pinaster*	EMF tolerance and uptake capacity of heavy metals: The EMF species capacity to adapt to heavy metal contaminated soils should guide an adequate EMF species choice for inoculating target plant hosts, to increase their growth under controlled greenhouse conditions.
Sýkorová et al. (2016)	Fly ash pollution/soil erosion	Prague, Czechia	Soil inoculation and field experiment (with fertilization)	Commercial EMF inoculum with multiple species	*Pinus sylvestris* *Quercus robur* *Tilia cordata* *Alnus glutinosa*	Native EMF capacity to self-colonize at the restoration site: Native EMF already present in the site are able to colonize target plant hosts with previous mycorrhizal inoculation in nursery not bringing any significant benefit.
Walker (1999)	Mining/heavy metal contamination	Sierra Nevada, CA, United States	Inoculation at nursery and subsequent field experiment	*Pisolithus tinctorius*	*Pinus jeffreyi*	EMF tolerance to heavy metals and metal uptake amelioration by the plant host: EMF inoculation of target plant hosts have higher rate of survival and growth, probably related to reduced uptake of potentially phytotoxic metals, particularly Mn and Al.

Different sources of degradation are considered (disturbance type) as well as globally distributed locations. Main EMF attributes considered in each of the studies from both nursery and/or field experiments are informed together with the plant hosts species and the EMF species evaluated.

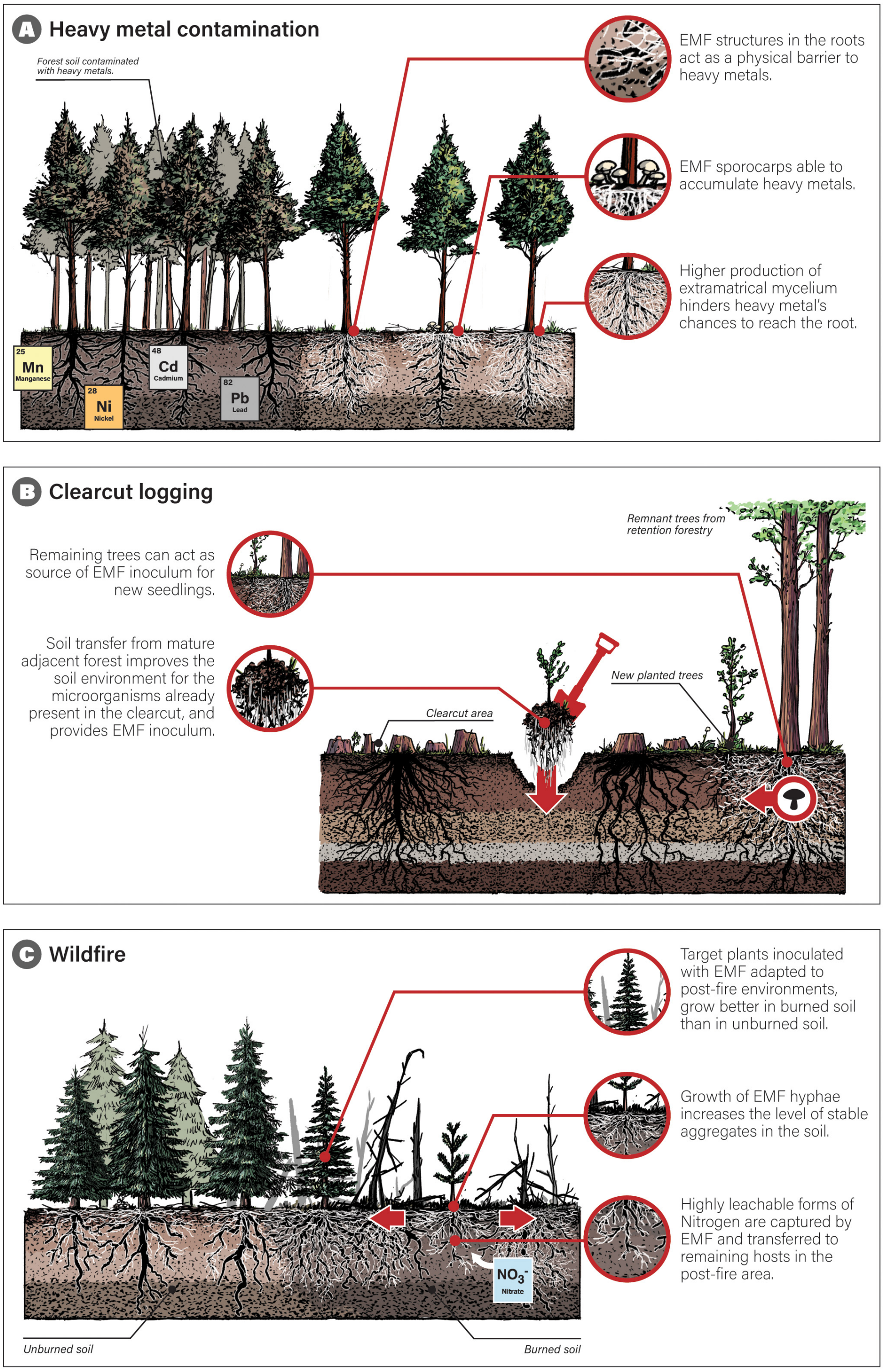

FIGURE 1 | Three different scenarios of temperate or boreal forest degradation and suggested modes of restoration that consider the use of ectomycorrhizal fungi (EMF). In panel **(A)**, specific host trees associated with heavy metal tolerant EMF are planted in forest soil contaminated with heavy metals. In panel **(B)**, retention forestry is presented as an alternative to clearcut logging, in which groups of mature trees are left intact and are able to offer new planted trees access to the existing mycorrhizal network, favoring establishment. Soil translocation from adjacent forest is a complementary option to improve soil conditions in the clearcut area. In panel **(C)**, EMF inoculated plants are planted in the post fire area. EMF traits help increase hosts' growth, soil aggregates' stability, and nutrients' transfer to other hosts nearby.

metals in those sites (Walker, 1999; Sousa et al., 2012, **Table 1**). All of the studies found better growth and survival rates of EMF-inoculated hosts compared to non-inoculated plants, although there were differences according to the EMF species inoculated (**Table 1**). This species-level variation in protecting host plants from heavy metal toxicity may be due to uneven distribution of specific macrostructure traits across EMF species. Some EMF species can be negatively affected by high levels of heavy metals, reducing the number of sporocarps (i.e., 'mushrooms') produced at increasing levels of soil heavy metal pollution (Rühling and Söderström, 1990). However, common EMF species like *Amanita muscaria* or *Suillus bovinus* are able to accumulate high metal contents in their sporocarps (Leyval et al., 1997; Luo et al., 2014, **Figure 1A**). The protective effect of EMF against metal toxicity is also related to fungal structures in the root acting as a physical barrier to metal uptake in plants (Donnelly and Fletcher, 1994, **Figure 1A**). EMF tolerance -or capacity to absorb- heavy metals is species-specific and might depend on the amount of extramatrical mycelium produced. EMF with higher production of extramatrical mycelium might offer better protection to the plant host and fewer chances for heavy metals to reach the root. Species of *Amanita, Paxillus, Pisolithus, Scleroderma, Suillus,* and *Rhizopogon* accumulate high metal concentrations in the extramatrical mycelium, with decreasing metal concentrations along the Hartig net to the root interior of the plant symbiont (Wilkins, 1991; Khan et al., 2000). The capacity to produce high amounts of extramatrical mycelium, together with the capacity to absorb heavy metals and the tolerance to contaminated soils, will necessarily condition the selection of appropriate EMF species for use in remediation (Khan et al., 2000). Evidence shows that the ability to restrict the entry of toxic metals into the plant's cell is partly dependent on the bioavailable metal concentration and the EMF species used (Khan et al., 2000; Sousa et al., 2012, **Table 1**). In recent years, several metal-tolerant isolates of EMF and associated hosts have been identified (Luo et al., 2014). The EMF species *Pisolithus albus* has been used as inoculant of ectomycorrhizal endemic hosts (*Acacia spirorbis* and *Eucalyptus globulus*) in tropical forests of New Caledonia degraded by mining activities, helping plant growth and acting as a protective barrier to toxic metals (Jourand et al., 2014). The restoration success in heavy metal contaminated sites is conditioned by successional interactions within the EMF species, and their ecological traits (e.g., dispersal, host preference, life history) (Kalucka and Jagodzinski, 2016). As both the plant host and the fungi mutually benefit in the ectomycorrhizal symbiosis, the use of plant-EMF pairs for restoration might be more effective than non-mycorrhizal plants or free-living soil microorganisms (Malajczuk et al., 1994; Leyval et al., 1997).

Soil Erosion

Eroded soils usually include physically and chemically harsh conditions for organismal growth, such as low water-holding capacity, low organic matter, and extreme temperature (Roose et al., 2006). Reforestation programs intending to protect against soil erosion, rarely consider the effect of soil microbiota on increasing soil stability and function, which might partially explain some of reforestation failures in eroded soils. We found seven studies that addressed some form of soil erosion, many of them after mining (**Table 1**). In combination with other restoration techniques (Löf et al., 2012), EMF inoculation or soil translocation enhances soil restoration and drives plant community development (Wubs et al., 2016). One of the key factors necessary to restore eroded soils is to reactivate microbial activity (Diaz et al., 1994). Many eroded soils have lost the topsoil, in which most microbial activity occurs, so for mycorrhizal plant hosts it is common to find low level of mycorrhizal infectivity (Powell, 1980). To restore this mycorrhizal activity, nursery inoculation of EMF species that tolerate the harsh conditions of eroded soils has proven to be effective (**Table 1**). Greater EMF activity can increase the level of stable aggregates in the soil due to the growth of fungal hyphae (Caravaca et al., 2002). Mechanical soil treatment (e.g., soil ripping) can encourage the root colonization of new seedlings by EMF, enhancing plant establishment and long-term survival (Bauman et al., 2013). EMF nursery inoculation improved the performance of conifers planted in oil sands reclamation areas and degraded gypsum soil (Rincón et al., 2007; Onwuchekwa et al., 2014). However, these effects are highly dependent on the EMF species inoculated. Even when inoculation with most EMF species tends to be beneficial for plants growth, some species can show no effects or even negative effects (Roldán and Albaladejo, 1994). Due to the absence of viable fungal inoculum in highly eroded soils, further tests are needed to explore the use of soil from adjacent areas as a source of native EMF inoculum. Naturally inoculated seedlings from the field could be transplanted to nursery pots with soil from eroded areas and planted together with new seedlings, which - once inoculated - can be used for reforestation.

Clearcut Logging

Clearcut logging can change the EMF community composition of forests (Jones et al., 2003). The removal of a major plant C source, together with physical and chemical changes in the soil, provoke a change in the composition of the EMF community, favoring those EMF species that are able to disperse into, establish in, or persist under these new conditions (Jones et al., 2003; Sterkenburg et al., 2019). Retention forestry (**Figure 1B**), a practice that has been implemented in forest management since just a few decades ago, is an alternative to clearcutting, by which a portion of the original stand is left unlogged to maintain the continuity of structural and compositional diversity (Gustafsson et al., 2012). Keeping patches of EMF trees is expected to favor the establishment of new seedlings near those patches, as EMF species abundance and richness depend on the amount of host trees retained (Sterkenburg et al., 2019). In these patches, seedlings can access the existing mycorrhizal network and a larger pool of soil nutrients, water, and potentially C transference from adult plants (Simard and Durall, 2004). The presence of hosts patches nearby can also act as a source of fungal spores, which can increase EMF colonization of new seedlings and hence their nutrient and water uptake (Colinas et al., 1994; Simard, 2009; Van Der Heijden and Horton, 2009, **Figure 1B**). The study we found addressing the use of EMF to restore clearcut logging sites (**Table 1**) reported that soil transfers from mature adjacent forests facilitate the formation of ectomycorrhizas by decreasing detrimental rhizosphere bacteria, creating a suitable environment for the organisms already present in the clearcut habitat (Colinas et al., 1994, **Figure 1B**). Alternatively to soil translocation, nurse plants that tolerate the harsh conditions present in a degraded environment can act as sources of EMF inoculum to facilitate the establishment of target plant species (Bai et al., 2009; Richard et al., 2009; Baohanta et al., 2012; Kennedy et al., 2012).

Wildfire

Wildfire is detrimental to most fungal species (Hart et al., 2005; Cairney and Bastias, 2007). However, several EMF species have been described as fire-adapted depending on the intensity and frequency of fire (Glassman et al., 2016). As it is described for seed banks, ruderal EMF species, can thrive after fire, taking advantage of their spore resistance, available resources and absence of potential competitors (Glassman et al., 2016). These post-fire fungi might be crucial for recruitment of new ectomycorrhizal plant hosts and increasing soil stability (Claridge et al., 2009). Moreover, while most soil N is lost through combustion, ammonium ($NH4+$) and nitrate ($NO3-$, which is highly leachable) can increase due to incomplete combustion and pyrolysis of organic matter (Wan et al., 2001). These forms of N can be captured by EMF and transferred to remaining hosts in the post-fire area (Claridge et al., 2009, **Figure 1C**). As the post-fire EMF community composition can greatly vary according to fire intensity, frequency, and environmental conditions (Dove and Hart, 2017), simple bioassays using seeds from the potential native hosts planted in soil from affected areas can be used to determine the EMF species that would potentially colonize first after fire (Glassman et al., 2016).

Post-fire EMF communities might passively re-establish as long as viable propagules of fire-adapted fungi are present in the soil (Glassman et al., 2016), disperse from adjacent areas (Horton, 2017), or remain present in less affected areas, including deeper soil horizons, as viable mycorrhizal networks (Palfner et al., 2008). However, active restoration might sometimes be needed after wildfire. The three studies we found regarding post-fire restoration actively inoculated EMF (**Table 1**). Due to inoculation with selected species of EMF in the nursery, the growth of *Pinus pinaster* in burned soil was promoted compared to unburned soil (Sousa et al., 2011; Franco et al., 2014). Likewise, inoculation with *Tuber melanosporum* improved the survival rate and the growth of aerial and root systems of *Quercus ilex* trees in post fire stands (Martínez et al., 2012). Nursery inoculation could provide long-lasting advantage in terms of growth to plant hosts planted in post-fire stands (Martínez et al., 2012; Franco et al., 2014). Similar to plant community restoration, active restoration should prevent and minimize stress upon remnant native EMF communities (e.g., avoid introduction of non-native EMF species or further soil erosion or anthropic disturbance, Claridge et al., 2009).

POTENTIAL USE OF EMF IN RESTORING SITES INVADED BY NON-NATIVE PLANT SPECIES

None of the papers we found used EMF to actively restore invaded or post-invasion plant communities (but see Patterson, 2019; **Box 2**). Although there is a high potential for active restoration of invaded communities using EMF, there is still a need for experimental evidence that test its effectiveness. Traditionally, restoration approaches have considered aboveground organisms that can be easily monitored over time, with soil biota generally being neglected (Wolfe and Klironomos, 2005). However, belowground microorganisms (such as EMF) are frequently a key mediator of forest invasion by non-native tree species.

Several studies, mostly from the Southern Hemisphere, have shown that many EMF species generally co-invade with non-native invasive woody plants (Nuñez et al., 2009; Dickie et al., 2010; Nuñez and Dickie, 2014). The most studied case is that of plant species in the Pinaceae and their co-invasion with non-native EMF (Dickie et al., 2010). The invasion of pine trees into the Southern Hemisphere is one of the most widespread invasions of non-native species on Earth, transforming native forests, grasslands, and shrublands into conifer-dominated forests (Simberloff et al., 2010; Nuñez et al., 2017). Pine trees obligately associate with diverse EMF communities in their native habitats, but pine invasion into native forests is consistently associated with colonization of the pine roots by a small number of non-native invasive EMF species (Nuñez et al., 2009; Hayward et al., 2015a,b; Policelli et al., 2019). In spite of being highly invasive, Pinaceae species are frequently planted for forestry (Richardson and Rejmánek, 2011). The use of non-invasive EMF as inoculants for new plantations can be an alternative to avoid or hinder the invasion of pine hosts. In regions such as South America and New Zealand, several Pinaceae species invade temperate forests of the native ectomycorrhizal tree species *Nothofagus* that is associated in turn with native EMF (Policelli et al., 2020). In those regions, EMF species themselves are starting to be considered the subject of possible invasion management (Dickie et al., 2016). Management of the mutualistic interaction between pines and EMF, instead of the species individually, seems to be the next approach to avoid further advance of the invasion.

After removal of invasive hosts, soil legacies are a major problem for restoring invaded forests. Apart from any change in soil biogeochemistry produced by the invasion, there are also EMF species capable of residing for decades in soil (Dickie et al., 2014). The use of native EMF as source of inocula that can help post-invasion soils recover and improve the establishment of native plants is being increasingly considered (Maltz and Treseder, 2015). Inoculation treatments either with soil from a reference community or with single EMF species - performed both in nurseries or in the field - have worked effectively for re-establishing and increasing the growth of native plants in restoration programs (Dulmer et al., 2014; Henry et al., 2015; Hudon, 2019; Patterson, 2019). Native plants that promote EMF proliferation may also assist in management of invaded forests.

Although EMF have not been directly manipulated for restoration projects in invaded ecosystems, invasion scenarios offer an opportunity to learn potential desired ecological traits of EMF that can be used for restoration in the native habitat (Hoeksema et al., 2020). The same EMF species that aggressively co-invade with Pinaceae trees in the Southern Hemisphere (Hayward et al., 2015a; Policelli et al., 2019) can be used to restore pine forests in the Northern Hemisphere due to their spore resistance and germination rates in the presence of the

BOX 2 | The Albany Pine Bush – An ongoing case study of forest restoration using EMF.

The Albany Pine Bush Preserve (APBP) located in Albany, New York State, United States, contains a fire adapted pine barren system. The community is a savannah-like habitat with Pinus rigida (pitch pine) as the dominant tree species. The community relies on fire which had been suppressed for decades and in its absence, Robinia pseudoacacia (black locust) invaded (**Figure B1**). R. pseudoacacia is an N-fixing legume that is associated with arbuscular mycorrhizal fungi.

FIGURE B1 | Sites at the APBP. Left panel: invaded community before black locust removal. Right panel: target open pine community.

The APBP is actively restoring the pine barrens through prescribed fires (Hayward et al., 2015a). The locust is removed by ripping up the trees and mechanically stirring the soil in an effort to kill off roots that would produce new shoots. After the locust is removed, the managers plant young pitch pine seedlings, which do not always establish.

To increase successful pine establishment, several pine seedlings were inoculated with spore slurries made from locally-collected *Suillus brevipes* and *Rhizopogon pseudoroseolus* sporocarps (Hudon, 2019; Patterson, 2019). Inoculation with live spore slurry improved seedling survival after outplanting ($F = 39.55$, $p < 0.001$, df 1,8, $n = 10$; **Figure B2**).

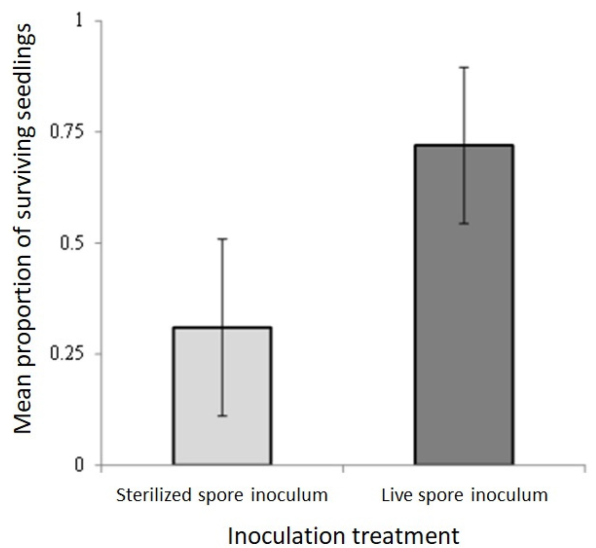

FIGURE B2 | Proportion of *Pinus rigida* seedlings that survived in the field inoculated with sterilized spore inoculum (light grey bar) and live spore inoculum (dark grey bar) of *Suillus brevipes* and *Rhizopogon pseudoroseolus*. Error bars show confidence intervals (95%).

hosts (Horton, 2017; **Box 2**). EMF can help to promote seedling survival by improving their resistance to stress, a trait that is likely to benefit reforestation programs over fast growth (Jacobs et al., 2015; **Box 2**).

LIMITATIONS ON THE USE OF EMF IN FOREST RESTORATION

Choosing suitable EMF species for restoration is not trivial (Trappe, 1977). Different results - in terms of plant survival and growth - can be obtained depending on the EMF strains and plant hosts used (Onwuchekwa et al., 2014; Sousa et al., 2014). Not all EMF are good candidates for restoration efforts. While some may not survive in the harsh environmental conditions at a degraded site, others do not produce long-lived propagules/spores that can be used as inoculum including many species of *Cantharellus, Russula* and *Tricholoma*. EMF should be considered for restoration efforts if they have life history traits that contribute to their success in early successional settings, such as the production of functional spore inoculum (Ashkannejhad and Horton, 2006; Horton, 2017), and include species of

Hebeloma, Laccaria, Pisolithus, Rhizopogon, Scleroderma, Suillus and *Thelephora* (**Table 1**). While some EMF can be inoculated with spores, many cannot. Even some species that are common in disturbed habitats might require growth of mycelial culture and direct inoculation of fungal plugs onto seedling root tips. The EMF that become established may remain at the site for years, so care must be taken to avoid introducing undesirable species for the habitat. In addition, the selection of EMF species that are not present in reference sites nearby could limit the success of restoration as they may not be adapted to local environmental conditions (Maltz and Treseder, 2015). Multiple inoculation experiments with EMF species that exhibit long distance exploration types such as *Scleroderma*, or *Pisolithus* (Agerer, 2001), together with species with the capacity to produce resistant spores (Bruns et al., 2009), and tolerance to harsh environmental condition (e.g., suilloid fungi) might be beneficial for target hosts. The list of EMF species tested for restoration and the empirical knowledge of EMF ecological traits are limited. Moreover, the introduction of novel EMF species or strains can cause unpredictable negative impacts to the ecosystem (e.g., changes in biogeochemical cycles, and facilitation of non-native plants' invasion) (Pringle et al., 2009). Native EMF should be preferred over non-native EMF species. In a comprehensive review, Azul et al. (2014) proposed a framework on how native EMF diversity and function could be valuable for sustainable habitat restoration in Mediterranean ecosystems. Even after choosing the EMF species to inoculate, growth and survival of plants depends on the way EMF are inoculated, even with the same set of species and in the same site (Walker, 1999, 2003). Nursery inoculation appears to be a cost-effective way to check for effective EMF colonization and initial plant growth before transplanting to the field (Teste et al., 2004).

Nursery and field results do not always correspond. Although inoculation with individual EMF species may be effective at a nursery, it is necessary to experimentally evaluate in the field the growth of plants inoculated with single and multiple EMF species. Some inoculated plants growing well in the nursery can have greater mortality than non-inoculated plants when transplanted to the field (Tosh et al., 1993; Roldán and Albaladejo, 1994; Rincón et al., 2007). Once in the field, EMF colonization of native plant roots might be dependent on the local soil environment. EMF inoculation of target woody plants might be hindered in sites that have suffered from long-term fertilization as farmlands, even when pre-inoculated in a nursery (Menkis et al., 2007). Fertilization of plants in the field tends to hinder colonization by EMF, diminishing growth and establishment of target plants (Sýkorová et al., 2016). If native compatible EMF are already present in the soil, EMF inoculated onto seedlings are often replaced by local fungi that are active in the soils. It should also be stated that mycorrhizal inoculation of hosts in nurseries before planting may not produce any significant benefit to the plant growth (Sýkorová et al., 2016).

Incorrect manipulation of the mycorrhizal component of the soil may have undesired cascading effects on the rest of the belowground and aboveground communities. Comprehensive knowledge of the system involved is required to prevent those undesired outcomes, yet is challenging to obtain. Further, good-intentioned, deliberate introductions of EMF species for restoration purposes increase the chances of invasions (Vellinga et al., 2009). Some EMF invasions can enhance the chances of non-native plants to invade (Policelli et al., 2019), or even be risky for human health if eaten, as the case of the deadly poisoning *Amanita phalloides*, likely introduced to North America associated with oak and pines (Pringle and Vellinga, 2006; Wolfe et al., 2010; Dickie et al., 2016). Furthermore, it is still unclear if tree hosts inoculated with EMF respond consistently across different ecosystem types, which may have consequences in the restoration outcome.

While EMF are known to be beneficial for plant establishment, a restoration effort involving these fungi is difficult to manage and monitor. One of the biggest issues is that the vegetative body of an EMF is microscopic, interacting with plant roots, belowground and out of site. Most restoration efforts will not have the resources needed to assess successful establishment of the fungi, particularly if there is no dedicated mycologist involved. Restoration efforts using EMF might benefit from selecting specific genotypes for restoration (**Figure 2**), following similar considerations for plants outlines by Lesica and Allendorf (1999). In that work, the authors proposed guidelines for selecting plant material for restoration that may work adapted for EMF: (1) Use local genotypes when feasible. (2) Initiate new populations with as many genotypes and as much genetic variation as possible (collect fungi from many local microhabitats). (3) Avoid strains that have been maintained in culture for long periods of time. (4) Use species with wide ecological amplitudes when feasible. (5) Use species with low dispersal capabilities to minimize the genetic contamination of resident populations (Lesica and Allendorf, 1999). These guidelines depend on the size and severity of disturbance, while the best choice for all sizes of disturbances is to use locally adapted EMF species (**Figure 2**). Although it is always wise to use multiple EMF species and genotypes within EMF species, this might be more relevant as the size and severity of the disturbance increases (**Figure 2**).

When the site is too degraded for locally adapted genotypes, the use of commercial inoculum emerges as possibility, especially in relatively small affected areas (**Figure 2**). Commercial inocula usually contain sources of N and P, and gels to maintain soil moisture, yet their composition needs to be carefully considered. Plants growing with many commercial inocula will probably grow bigger compared to non-inoculated plants (Tarbell and Koske, 2007) and the use of commercial inoculants to restore mycorrhizal communities in soil has received increasing attention in different parts of the world. However, because of the risk of introducing non-native fungi, or even the use of widely distributed fungi (e.g., *Glomus* spp.), commercial inoculants have been discouraged (Heneghan et al., 2008; Dickie et al., 2016). In addition, many commercial inoculants are not effective in terms of mycorrhizal colonization of roots; sometimes very few, if any, might be colonized by mycorrhizal fungi. If no roots are colonized, such products risk creating a negative public opinion of mycorrhizal inoculants (Tarbell and Koske, 2007). When using commercial inocula in a restoration plan, the degree of mycorrhizal infection should be monitored. One must also keep in mind that the fungi that work best in controlled settings

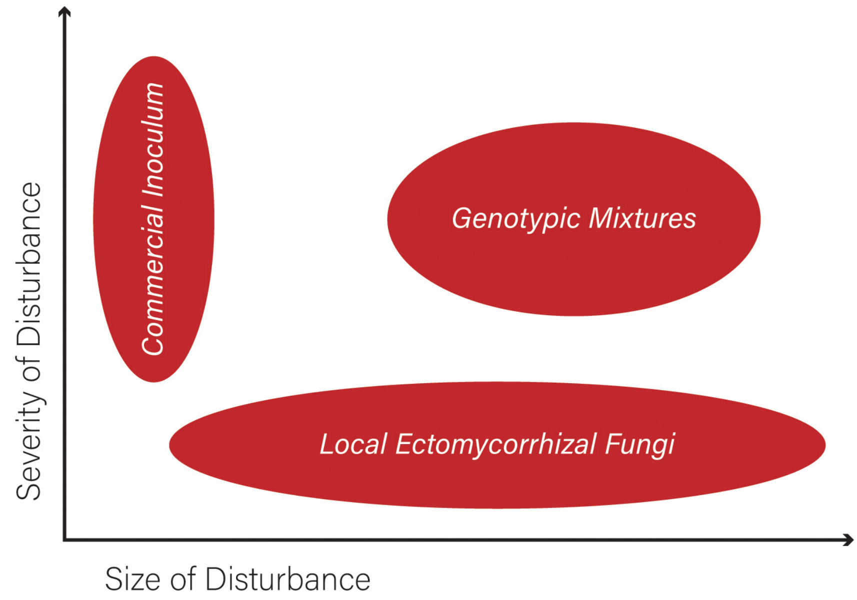

FIGURE 2 | The severity and size of a disturbance will impact the use of ectomycorrhizal fungi in a plant restoration effort. The best choice for all sizes of disturbances is to use locally adapted EMF species. As one moves to more severe disturbances, it may be necessary to use commercial inoculum that is more generally adapted because the site has been too degraded for locally adapted genotypes. As the size and severity of the disturbance increases it is necessary to use multiple EMF species and as much genetic variation as possible within species (e.g., collecting fungi from many local microhabitats) to increase the chances of restoration success. Adapted from Lesica and Allendorf (1999).

needed to generate commercial inoculum may not be best adapted for a restoration site. *Suillus* is commonly included in commercial products and is an excellent choice for restoration involving pine. However, it is specific to pine and will not support establishment of angiosperms such as oak, chestnut or eucalyptus. Indeed, all EMF have varying degrees of specificity, both in their compatibility with host plants (Molina et al., 1992) and tolerance to environmental conditions (so-called ecological specificity; Harley and Smith, 1983).

Using EMF for restoration may not always act synergistically with other restoration actions. Common practices of forest restoration such as reintroducing fire using prescribed burns or thinning, for example, may result in a reduction of EMF species richness, which can in turn translate into poor tree survival and slow stand recovery (Smith et al., 2005; Bastias et al., 2006) together with a reduction in fine root biomass (Hart et al., 2005). Several EMF genera are known to be resistant to disturbance and are expected to be the first taxa to colonize recruiting hosts (Baar et al., 1999; Stendell et al., 1999; Glassman et al., 2016). Nevertheless, target plant species survival and growth can also be negatively affected due to inadequate site preparation techniques. To help counteract this, mechanical methods such as scarification, mounding and subsoiling are used to prepare the soil (Löf et al., 2012). These methods have multiple impacts in soil physical, chemical, and biological properties depending on their intensity and frequency (Löf et al., 2012). In areas with soil compaction due to anthropic degradation (e.g., post mining soils, areas of clearcut logging), soil mechanical treatments enhancing EMF colonization could aid in the establishment and growth of target plants if sources of compatible EMF are nearby (Bauman et al., 2012; Pec et al., 2019). However, intense mechanical treatments such as deep ripping may extensively disrupt existing mycelium networks. Relatively simple greenhouse experiments could address the interactive effects of these mechanical methods and the use of EMF to determine the necessity and time to apply both restoration techniques in the same site (Bauman et al., 2013). Whether the target of restoration is re-establishing certain plant species or the entire plant community, restoration programs should consider the ecological processes and interactions both above and belowground upon which the persistence of that target community is contingent.

RECOMMENDATIONS FOR FUTURE RESEARCH

A limited number of EMF species have been tested for temperate and boreal forests restoration purposes (**Table 1**). Future experimental tests should gather evidence from other species and their ease of use as inoculants in terms of plant hosts' growth and survival. Inoculation of *Pinus halepensis* hosts with *P. tinctorius* improved the performance of the seedlings and was involved in soil aggregate stabilization in a reforestation program in a semi-arid system in Spain (Caravaca et al., 2002). This EMF has also proven effective in restoration plans using other hosts, such as *Quercus suber* (Sebastiana et al., 2013). However, *Pisolithus* is also characterized as a poor competitor, commonly displaced by other ECM fungi shortly after field planting (Bauman et al., 2013). Other more specific EMF species, such as suilloid fungi for pines, seem to be effective (**Table 1**), in part due to their tolerance to harsh environments. Generalists EMF might also be effective in restoration, as they are shared by different ectomycorrhizal tree host species and can aid in the establishment and growth of a focal species near other tree species already present in the site (Bauman et al., 2012). EMF genera that are effective in nursery inoculation include *Laccaria, Hebeloma, Thelephora, Rhizopogon, Suillus, Cenococcum, Scleroderma, Pisolithus* (Trappe, 1977, **Table 1**) and should be further evaluated in field restoration plans. Other EMF genera need to be explored in terms of their inoculation capacity and effectiveness in the field (e.g., native symbionts with native plants in Southern Hemisphere native forests). Exploring other EMF genera will also expand the set of plants hosts evaluated for restoration, which seems to be limited to a set of species mostly in the Pinaceae and Fagaceae families (**Table 1**).

In addition to promoting above- and below-ground biodiversity, inoculation with EMF to ensure host establishment can be economically profitable. *Quercus ilex* individuals inoculated with *Tuber melanosporum* had a higher survival rate and growth that those non-inoculated in a post-fire restoration program in NE Spain (Martínez et al., 2012). *Tuber melanosporum* is widely known for its gastronomic use and commercial value. Other less expensive - but also edible - EMF (e.g., some *Suillus* species) have also been used as inoculants and provide the extra economic benefit of an edible species in this restoration context (**Box 2**). Commercial edible EMF, as with other non-timber forest products, can help local communities become involved and support restoration programs in the medium and long term.

Incorporating EMF in restoration efforts can help increase the rate of restoration success, and restoration goals could be reached in a shorter amount of time after disturbance (**Figure 3**). Restoration success is hard to define and may vary based on what the restoration goals are. Most of the studies addressing the role of EMF in restoration examined root tips for EMF colonization and measured height or survival of seedlings over a period of time. This may not relate back to the whole picture of a habitat reaching a pre-disturbance state, in an attempt to answer an ecosystem's change over time (Box 1). It is difficult to maintain long term studies, particularly if there is a need to quantify the success of habitat restoration. Martínez et al. (2012) measured EMF presence 10 years after planting inoculated seedlings but this amount of time was not typical for other studies listed in **Table 1**. Most completed sampling after 5 years and six were completed after a year or less (Colinas et al., 1994; Roldán and Albaladejo, 1994; Sousa et al., 2011, 2012; Onwuchekwa et al., 2014; Patterson, 2019). If the goal is to get a functional and sustainable plant community of choice on the site, it can take longer. Explicitly identifying the target outcome (i.e., re-introduction of certain plant species, reduction of contamination or erosion in the soil, restoration of certain ecosystem functions)

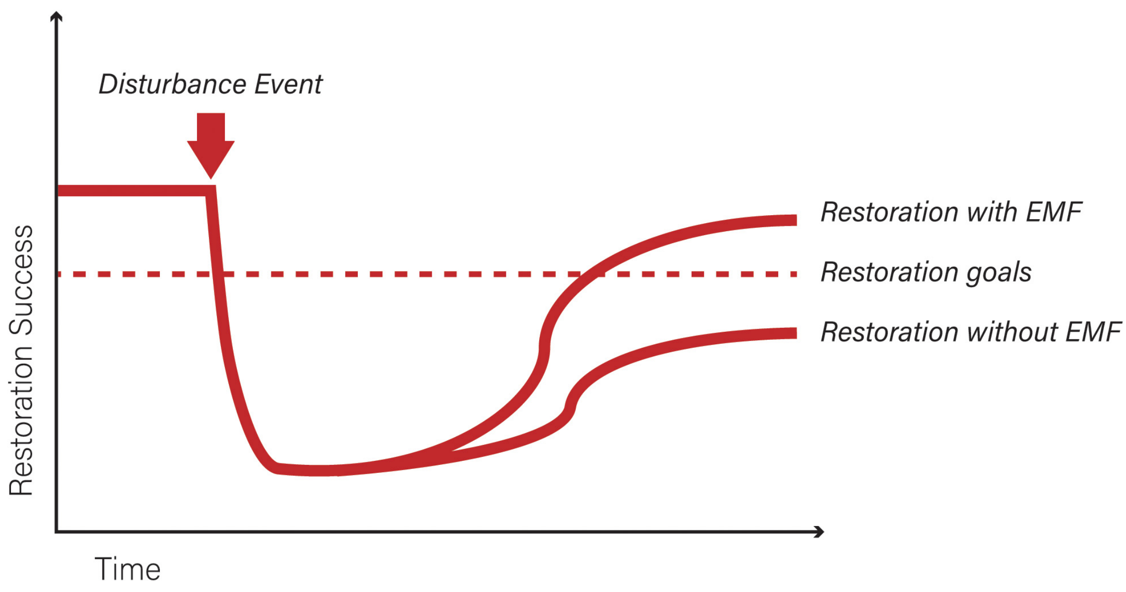

FIGURE 3 | Conceptual model showing restoration success over time. The arrow indicates a disturbance event. The dotted line representstargeted restoration goals at the time of implementation. After a natural or anthropic disturbance event disrupts the original community, a restoration plan is implemented, establishing restoration goals (e.g., restoring specific ecosystem functions, reintroducing a particular species of interest). It is often impossible to recreate the pre-disturbance conditions and there is often a time lag between the initiation of restoration activities and the habitat response to that restoration plan (due to species or communities time to reoccupy suitable restored areas, and time to achieve measurable restoration effects). Although the shapes of the curves and the length of disturbance and success of restoration might be variable and difficult to measure, incorporating suitable EMF in restoration efforts can help increase the rate of restoration success due to increased survival and growth of specific plant hosts, and the improvement of soil properties (e.g., increase soil stability, decrease heavy metal toxicity). Restoration goals could be reached in a shorter amount of time after disturbance compared to a situation in which EMF are not considered and restoration fails to achieve the initial goals. Other trajectories not shown in the figure are possible: if the EMF species are not properly chosen, for example, long-lasting effects might not be attainable and instead of reaching a *plateau* when restoration goals are achieved, the curve would start decreasing. Monitoring over time is necessary to avoid possible undesired outcomes.

will improve the predictions of the time needed for restoration after disturbance. Additionally, the advance in molecular tools is an advantage in EMF research that aims to link EMF community composition to their role in ecosystem functioning (Horton and Bruns, 2001; Koide et al., 2014; Bonfante, 2018). Future research that focuses on determining the functional role of different EMF species for restoration purposes and understanding the context dependency of these roles in terms of the rest of the soil community will aid restoration efforts (Aerts and Honnay, 2011). Newly available molecular tools to quantify microbial diversity, combined with detailed measurements of forest functioning are likely to increase our insights in how to apply belowground biodiversity for restoration purposes.

All the studies we found using EMF for temperate and boreal forests restoration were performed in a limited number of locations (**Table 1**). Experimental evidence of restoration successes or failures should be published from other regions and ecosystems. Particularly in many countries of the Southern Hemisphere where economic limitations may hinder the possibilities of successful restoration programs, EMF offer an economical, sustainable, and long lasting alternative for temperate forest restoration. Moreover, environmental gradients should be further explored to address restoration success variability and suitability of EMF-host pairs. Identifying organisms best adapted to specific environmental and biotic conditions and assessing the potential for managing these organisms are the first steps to introduce the idea of a living soil in restoration, as part of an expanding view of forest ecosystems (Stanturf et al., 2014; Jacobs et al., 2015).

CONCLUSION

In this article, we address the conceptual incentive and the empirical evidence evaluating EMF as a potential tool for restoration of forest ecosystems. Although there is no "magic bullet" for effective restoration, there is opportunity to use soil organisms as "tools" to achieve restoration success. Restoration projects are not always successful and results are highly context dependent. The relatively low number of studies actively using EMF to restore temperate and boreal forests hinders our capacity to better describe the context dependency of the effectiveness of this restoration technique. At the same time, it emphasizes the necessity of more experimental studies in different climatic zones and disturbance contexts. However, there is evidence that restoration of the native microbiome improves the establishment of plants that are often missing from restored communities (Koziol et al., 2018). An increasing understanding of EMF diversity and functional traits might enhance the ability to better choose and experimentally test which EMF species would work in each restoration scenario. In nursery inoculation and field experiments, native EMF should always be prioritized to avoid possible undesired outcomes (e.g., EMF invasions). Restoration programs considering plant–EMF interactions have been mostly applied in areas affected by soil erosion, heavy metal contamination, wildfire, and clearcut logging. Some of these disturbances are explored to a much lesser extent than others and future experimental approaches should explore other regions and environmental gradients affected by these and other possible disturbances. We outlined some possible undesired outcomes and limitations of the use of EMF in forest restoration, highlighting the idea that not acting does not entail a solution. The use of EMF in forest restoration can be complementary to the increasing application of adaptive management, in which learning and resource management act simultaneously in a context of uncertainty (Jacobs et al., 2015). We suggest a more holistic view of forest management that considers a belowground perspective of forest restoration. Particularly for boreal and temperate forest restoration, we offer evidence that EMF should be considered as a management tool to improve the chances of success of future restoration programs.

AUTHOR CONTRIBUTIONS

NP and JB conceived the study. NP collected the data and led the writing of the manuscript. NP, TH, AH, TP, and JB participated in data interpretation and revised the manuscript. All authors contributed to the article and approved the submitted version.

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