Chapter

Impacts of Invasive Plants on Soil Fungi and Implications for Restoration

Brooke Pickett, Mia Maltz and Emma Aronson

Abstract

Biological plant invasions impact the function and biodiversity of ecosystems across the globe by displacing native plant species and altering the physical and chemical soil environment. While much is known about direct competition between invasive and native plants, ecologists have just begun to uncover the less obvious impact of plant invasion: changes to the soil fungal community. Fungi are important to the survival of many plant species and an integral part of a healthy soil system. Arbuscular mycorrhizal fungi are plant mutualistic symbionts that associate with many species and provide necessary services, such as increasing surface area for root water absorption and resistance to pathogens, while ectomycorrhizal fungi play an equally important role and are critical for plant nutrient acquisition in boreal and temperate forests. Invasive plants are altering the soil fungal community in ways that indirectly impact the structure of native plant communities, sometimes for years after the invasive plant has been removed from an area (i.e., legacy effects). These changes make restoration especially difficult in areas from which long-term plant invasions have been eradicated; in some cases these changes can be so severe that even with active management, they take months or decades to reverse.

Keywords: mycorrhizal, fungi, roots, legacy effects, restoration, microbial, invasion

1. Introduction

The global scale of plant invasion means we need to understand it better at all levels in order to prevent further damage. While much research has been conducted about the ecosystem impact of invasive plants, ecologists have recently begun to uncover a less obvious, but important, consequence of plant invasion: changes to the soil fungal community.

Fungi are ubiquitous and the principal decomposers of organic debris in ecosystems all around the world [1]. They are essential to decomposition and nutrient cycling in most intact environments, ranging from unicellular aquatic chytrids to large mushroom fruitbodies with extensive mycelial networks. They acquire their food by exuding enzymes into their environment, breaking apart the bond structures in complex compounds, and subsequently absorbing the dissolved nutrients and molecular components. Some fungi exist as symbionts of plants and animals while others exist as free-living cells. Symbionts can interact with their host as mutualists, parasites, or in a way that does not affect the host (commensalism) [1]. Commensalism, in this context, not only includes symbionts but also free-living microorganisms performing nutrient transformations critical to plant growth, such as nitrification and denitrification [2].

Fungal mutualists interact with plants through mycorrhizal symbiosis, a symbiotic association between fungal hyphae and the roots of a vascular plant that can be characterized as either arbuscular mycorrhizal, ectomycorrhizal, or ericoid [3]. These mycorrhizal fungi grow in the rhizosphere of the plant and can be either intracellular (arbuscular mycorrhizal fungi; AMF) or extracellular (ectomycorrhizal; ECM). Plants and their symbionts communicate through molecular and genetic feedback during which fungi provide growth-limiting nutrients, such as nitrate and phosphate [3], and even facilitate plant-to-plant exchange of nutrients and carbohydrates [4]. These plant-fungal associations are extremely important to the survival of a majority (~90%) of all plant species [52].

When invasive plants are introduced to a healthy ecosystem, they can disrupt fungal mutualistic associations with native plants. Moreover, plant invasions may even prevent these mutualistic associations from occurring by altering soil nutrient dynamics, changing soil food webs, or introducing plant pathogens [2, 3]. Although not always negatively impacting mutualisms with native plants, these changes brought on by plant invasion can last for years [2, 4–10] after the invasive plant has been removed and are termed “legacy effects” [13]. These legacy effects are normally defined as the abiotic and biotic impact of a species that persist long after the invasive species has been eradicated or extirpated from an area [8].

Studies focused on understanding the legacy effects of invasive plant growth on native plants can have either similar or conflicting results, largely dependent upon the native and invasive species studied [14]. As a result, many suggestions for improving soils after invasive species removal have been anecdotal, and are context-dependent.

In this chapter, we will discuss how invasive plants may change the abundance or diversity of three important fungal symbionts (arbuscular mycorrhizal fungi, ectomycorrhizal fungi, and fungal pathogens), as well as the implications these changes may have for ecosystem health. We will finish off the chapter by discussing restoration efforts designed to ameliorate fungal legacy effects of invasive plants.

2. Biotic impact of invasive plants

Plant-soil interactions can be abiotic or biotic, meaning that plant composition can alter the chemical composition of the soil or the microbial composition of the soil and vice versa. Not until 1985, however, did papers linking the words plant and soil begin to appear in the BIOSIS database. Since then, papers about plant-soil interactions have appeared at a rate of 3500 per year [2]. So while the field is relatively new, it is growing quickly and becoming more diverse.

Early investigations of plant-soil feedbacks focused on physical properties of the soil, such as texture, water content, and temperature. Researchers then began investigating the chemical and biogeochemical components of plant-soil feedbacks, such as the pH, carbon, and nitrogen content of soils [2]. Currently, there is more focus on the role of microbes in regulating and responding to plants and the larger environment. This increased focus on microbes is due to their critical importance to the ecology of all macro-organisms: they are major decomposers in all ecosystems, important to the survival of most plant species, and an integral part of both carbon and nitrogen cycles.

Many studies have demonstrated shifts in microbial communities due to invasive plant growth [4, 12–17]. However, the phenomenon of *fungal* shifts in response to invasive plants is less understood, and potentially has many implications for maintaining biodiversity and function of invaded ecosystems. Throughout this section we will explore the ways in which invasive plants alter the fungal community (**Figure 1**).

2.1 Arbuscular and ectomycorrhizal fungi

Fungal hyphae, or collectively the mycelium or mycelial network, are filamentous strands of fungal cells which compose the main body of the fungus, and the fungal vegetative structure that is often branching and filamentous [20]. In soils, fungal hyphae grow throughout the soil matrix, with the direction of apical growth (from the apex to the hyphal tip) often dependent on an environmental stimulus. These hyphae exhibit a variety of morphological structures and functional modifications. Arbuscular mycorrhizal fungi (AMF) form arbuscules, small branching structures within cortical root cells, which are the sites of the bi-directional exchange of carbon and nutrients, such as phosphorus, between the plant and fungi [20]. Ectomycorrhizal fungi similarly exchange nutrients with plants, but they form a dense hyphal sheath that surrounds the root surface, rather than penetrating the root cells [21] (**Figure 2**). This mutualism provides a fungus with carbohydrates and the plant with an increased surface area for water and mineral absorption.

Arbuscular mycorrhizal fungi are obligate plant symbionts. These AMF are arguably the most common plant mutualistic symbionts, consisting of at least 145 groups [22]. They associate with most plant species and are especially important for the uptake of phosphorus [16, 18], an integral nutrient for plant growth. Over the years, researchers have discovered that AMF not only increases plant access to phosphorus, but they also provide resistance to pathogens [18, 19], stabilize soil

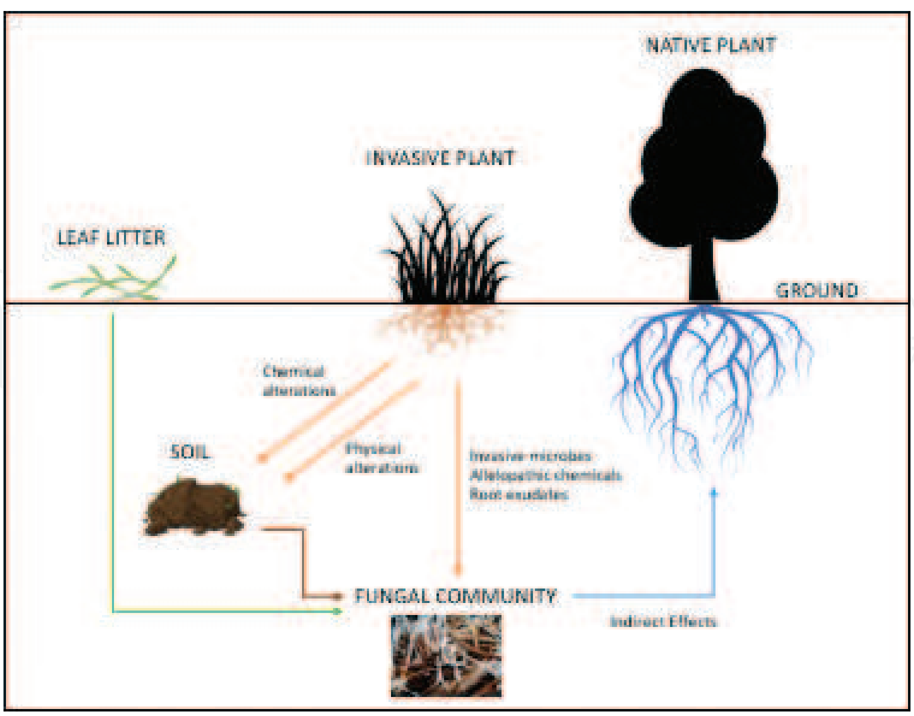

Figure 1.
Diagram showing the biotic impacts of invasive plants. Orange arrows: *the invasive plant alters the chemical and physical soil components, which has an indirect effect on the fungal community composition. The invasive plant directly affects the fungal community through introduction of invasive microbes, allelopathic chemicals, and root exudates.* Green arrow: *leaf litter can alter the fungal community composition if the invasive plant leaf litter has a different quality (C:N) than that of the native plant leaf litter.* Blue arrow: *all of these alterations to the soil fungal community have indirect effects on the growth of native plants.*

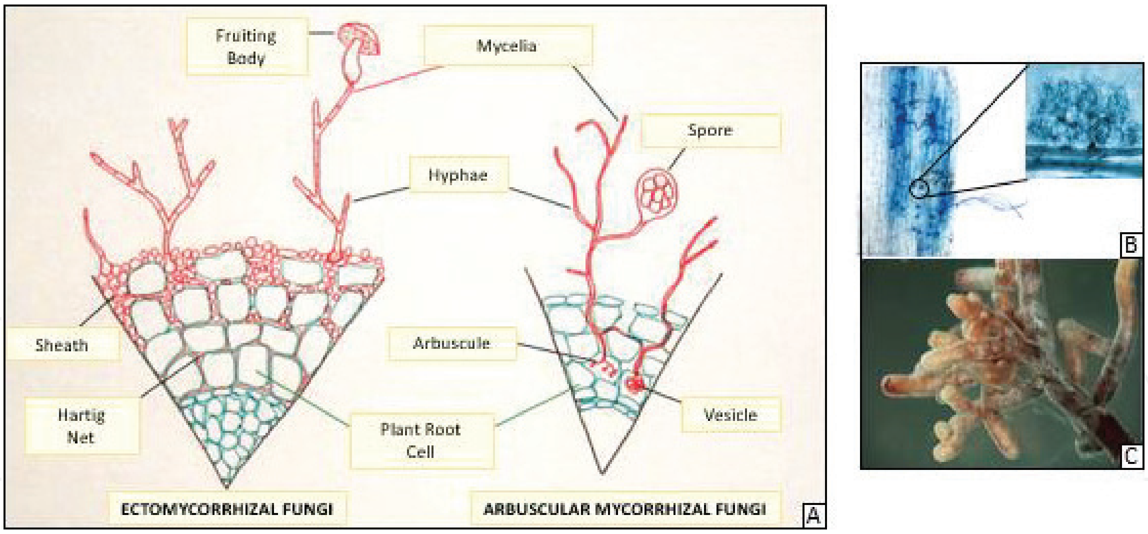

Figure 2.
(A) Diagram depicting the similarities and differences between ectomycorrhizal and arbuscular mycorrhizal fungi. (B) An arbuscule inside of a plant root. (C) Ectomycorrhizal fungal hyphae growing on a plant root.

aggregates [23], alter plant communities [22], and even ameliorate the allelopathic effect of some invasive plants [24]. Most AMF are generalists, meaning they associate with many plant taxa, while others are specialists, and associate with only one or merely a few plant taxa.

The widespread distribution and low host-specificity of most AMF suggests that when plants invade a healthy soil system, they can readily form associations with AMF. Since most invasive plants can probably form arbuscular mycorrhizas [25], it is not surprising to find that numerous opportunistic invasive plants also associate with AMF to their own advantage [26]. When associating with fast-growing, small-spored fungal taxa, such as *Glomus*, which can colonize via mycelia fragments, an invasive plant may be even more likely to thrive [27]. These associations with generalist AMF may allow invasive plants to outcompete and displace native plants which are either non-mycorrhizal (such as *Brassica* spp.), weakly mycorrhizal, or do not form associations with generalist AMF, in contrast to the generalist invader. One recent example of such an invader is *Vincetoxicum rossicum*, a forb that displaces native plants and was found to associate with four different AMF subgroups (*Glomus intraradices*, *G. caledonium*, *G. fasciculatum*, and *G. mosseae*), which are highly infective and remarkably efficient at phosphorus uptake. These same subgroups, however, were absent from the rhizosphere of each native plant growing within the invasive plant patches [27]. This finding suggests that the invasive plant's ability to associate with fungal generalists allows it to thrive and may improve its ability to displace native plants.

Some invasive plants have the ability to degrade local mycorrhizal fungi, a finding termed the "Mycorrhizal Degradation Hypothesis" [28] (**Figure 3**). Degradation of local AMF can change the soil in ways that hinder native plants and help invasive plants. Examples of this include *Alliaria petiolata*, a non-mycorrhizal plant, which has been known to produce glucosinolates which are potentially toxic to AMF, and *Myrica faya*, a plant which carries nitrogen fixing microbes, from the genus *Frankia* along with it to the invaded range [29].

While researchers have only just begun exploring the impact of invasive plant species on AMF abundance [25–27], it is evident that invasive plants can have the potential to either increase [14, 28, 29] or decrease [29, 30] the abundance and diversity of AMF. Increased AMF abundance with invasion may happen when the native intact plant community naturally associates with fewer AMF taxa than the invading mycotrophic (mycorrhizal) plants [4, 14, 24, 31]. In fact, if the invader is mycotrophic, a monoculture of the invasive plant may still harbor a more species-rich AMF

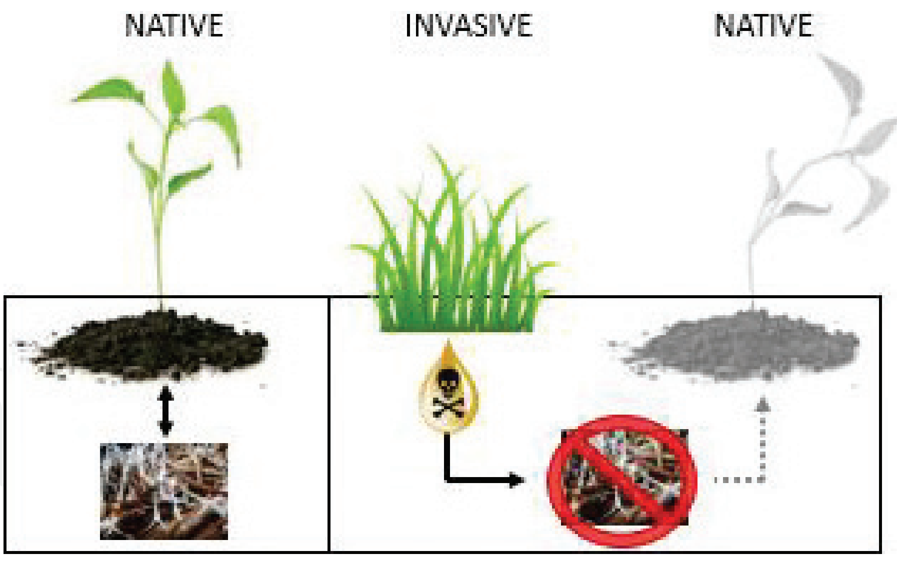

Figure 3.
Diagram illustrating the mycorrhizal degradation hypothesis. In the left panel, we see a healthy native plant in a mutualistic relationship with AMF. In the right panel, the invasive plant is producing a chemical exudate that eliminates beneficial fungi, thereby preventing fungal association with the native plant and eventually native plant death.

community than a diverse community of native plant species [17]. This increased abundance of AMF by the invader may actually feedback to increase invasion [36]. However, if the invading plant is non-mycorrhizal, then AMF abundance and diversity will decrease relative to pre-invasion soil [37]. A recent comprehensive field study [32] compared AMF abundance in soils invaded by one non-mycorrhizal and two mycorrhizal plant species. All three invaders reduced AMF abundance and richness, but the non-mycorrhizal plant reduced AMF abundance and richness to a greater extent. However, this pattern is not always so evident: if an invader is mycotrophic, but not a good host for AMF, then it may actually decrease the AMF abundance [33, 34]. Certain invasive plants may associate with particular groups of AMF, which may be different than those hosted by local native plants [39]. In these cases, invasion could subsequently bolster the abundance of some AMF groups, while decreasing the diversity or abundance of others.

In the presence of invasive plants, some studies show shifts in either AMF diversity [11] or from fungal specialists to generalists [3, 35], as well as differences in the prevalence of fungal versus bacterial utilization of leaf litter [11]. However, the identity and functional group status of both the native and invasive plant may dictate their effects on AM fungal symbionts. For instance, a recent meta-analysis [31] reported that invasions may not necessarily cause a shift in AMF associations, unless the native and invasive plant are in different functional groups. If an invader decreases AMF abundance or only increases the abundance of the particular AM fungal associate, then this could negatively impact native plant communities which are dependent on AMF for survival [31]. Changes to soil AMF abundance and diversity may not be short-lived; in fact, they could last long after the invader is gone [41]. Such biotic legacy effects can occur when plant-soil interactions are altered by invasive plants for long periods of time.

The timing of AMF response to invasion is still largely a mystery [42]. A recent meta-analysis [31] reported that AMF colonization of native plants may decrease due to legacy effects of invasive plants. However, it is unclear how quickly these legacy effects occur or attenuate after an invasive plant is removed, as well as how soon the community may return to the structure and functioning of the previously native state [42]. In certain instances, after an invasive is removed, any changes in AMF abundance and diversity are fleeting, because differences in abundance and richness return rapidly with the return of the native vegetation type [14, 38]. In contrast, in other studies [37] even a highly mycorrhizal invasive plant may not rapidly alter the AMF community, even after 29 weeks. Another study shows some recovery of AMF communities 6 years after the removal of an invasive known to decrease AMF abundance [13]. In some cases invasion can lead to the development of a novel AMF community over decadal time scales [30, 37, 39]. Overall, the recovery of the AMF community could take a long time. Furthermore, shifts in AMF may be dependent on an invasive plant's functional traits [39–42], which may ultimately be the best predictor for the extent of AMF response to invasion, and subsequent recovery.

Although AMF and other groups of mycorrhizal fungi, such as the ectomycorrhizal fungi (ECM or EM fungi), are phylogenetically distant [45] and functionally distinct, they both play key roles in ecosystem functioning. In boreal and temperate forests, ECM are facultative symbionts that play an important role in plant nutrient acquisition [46]. In fact, ECM take up about 80% of all plant nitrogen in boreal forests [47]. However, the impact of invasive plants on the soil composition of ECM has not been well studied [48]. The few papers that do tackle this issue have either found inhibition of ECM in the presence of a non-mycorrhizal invader [43–45] or suggest that an invasive plant may elicit an allelopathic effect on EM fungi [50]. Similarly as with AMF, ECM associations with native plants can be inhibited by invasive plant presence [49].

Invasive plants also introduce invasive AMF and ECM into the invaded range. Very little is known about the invasion process of AMF, but we do know that AMF propagules can be transferred long distances by wind, water, and agriculture [51]. When AMF is introduced to a new area, it spreads very slowly from the point of introduction, but can persist for up to a several years in the soil without a host [51]. Introduction could be problematic if the AMF are generalists and associate with invasive plants; in these cases it may not have an overall negative impact on an ecosystem that already harbors AMF. Normally ECM are beneficial to plants, but they have been shown to cause damage to invaded ecosystems by competing with native fungi, facilitating in the co-invasion of trees [52], and changing the soil foodwebs [53]. It is still unknown, however, what effect these invaders have on native host physiology and native fungal communities.

2.2 Fungal pathogens

Soil pathogens contribute to the spatial and temporal patterns of natural systems through negative plant-soil feedbacks [54] and may influence plant diversity by suppressing dominant plants [55]. Certain pathogens target either a group of related plant species or only one host plant genus.

Increase in global trade and the subsequent movement of plants has increased the number of introduced plant species and the pathogens they carry [56]. Some invasive pathogens have been introduced intentionally as biological controls [57], but most may be introduced inadvertently over trade routes. The fact that fungi are small and inconspicuous may be a major factor in their success as invaders and may be why these pathogens can spread faster than the host plants that carry them.

Pathogens brought over by invaders have been shown to decimate native plant populations. The lack of host resistance to invasive pathogens has caused severe environmental and agricultural damage in invaded areas [1]. Some examples of pathogenic microbes, often studied by plant pathologists and mycologists, are *Phytophthora cinnamomi* which infects Eucalyptus trees in Australia [58], *Armillaria luteobubalina* which has killed off 38% of plants in coastal ecosystems [59], *Phytophthora ramorum* which has infected more than 70 plant species in California and causes sudden oak death [60], and *Phytophthora kernoviae* which is the latest of many *Phytophthoras* recently found in the UK [56] (**Figure 4**).

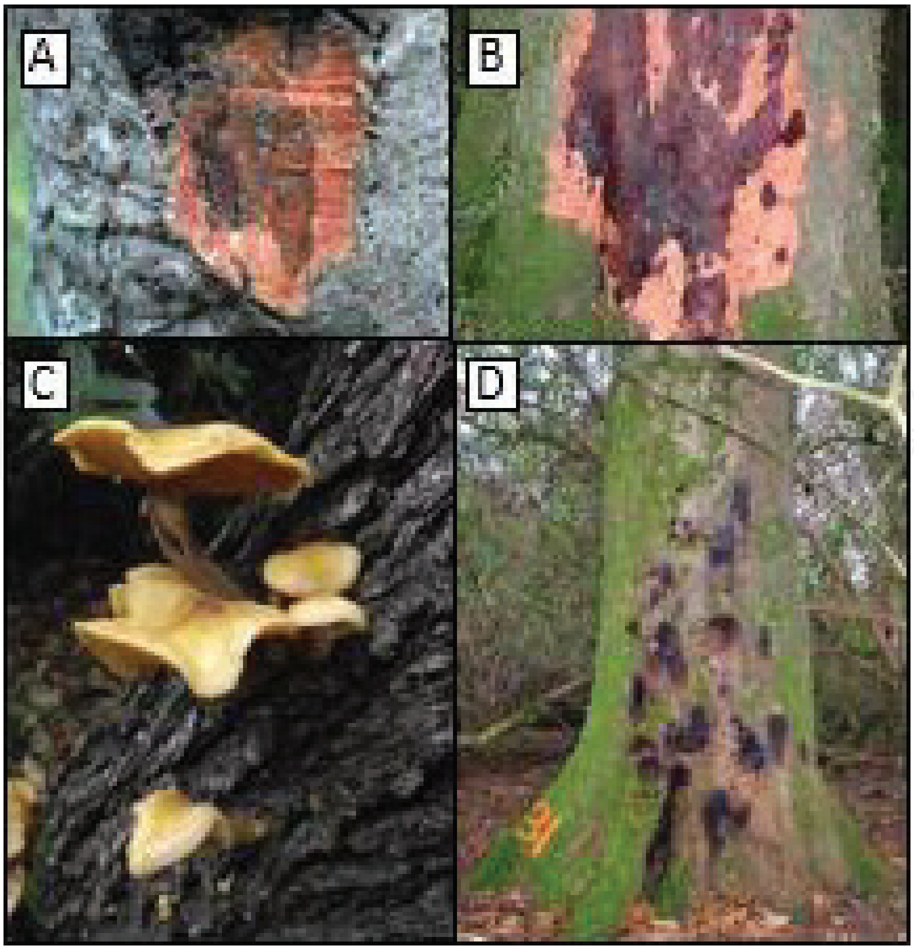

Figure 4.
(A) Phytophthora cinnamomi, *(B)* Phytophthora kernoviae, *(C)* Armillaria luteobubalina, *and (D)* Phytophthora ramorum.

Most studies concerning the spread of invasive fungal pathogens focus primarily on agricultural rather than natural systems. In a majority of papers, the invading pathogen that causes a devastating agricultural epidemic are those that coevolved with crop plants and were somehow reunited with their host [1]. The most well-known example of this is the Irish potato famine caused by *Phytophthora infestans*. In contrast, in natural systems, most harmful invasive pathogens did not coevolve with the plants they infect so the host plants have never been exposed to the pathogen before [1].

The main body of research that does focus on invasive pathogens in natural systems primarily deals with invasive forest pathogens. North American forests are continually threatened by invasive pathogens and several species of trees have already been essentially eliminated by them. The best example of this is the chestnut blight which killed off most of the mature native chestnut trees in the northeast US in only 30 years [61], replacing them with a variety of other hardwood species. Pests and pathogens may be even more harmful to these hardwood forests than the invasive plants that carried them there [62], with over 20 invasive pathogens infecting forests in the US and Canada [63].

Invasive pathogens in forest ecosystems are currently in the process of removing several foundation tree species that control productivity, water levels, forest structure, and microclimate [64]. When an entire species of tree is wiped out or an entire life stage or size class of tree is eliminated, the forest ecosystem can change dramatically. The loss of these species can negatively impact nutrient fluxes, water movement, biodiversity, and food webs [65]. The indirect effects of these species losses are difficult to calculate and could extend for multiple forest generations. If a relatively minor tree species is lost, the impact of the invasive pathogen may actually be small, but if a keystone species is lost there could be long-lasting cascading effects [64]. It is important to note that not all introduced pathogens are harmful to these forests [66], but more research is needed to identify those that are harmful before they spread.

The damage wrought by invasive pathogens is clearly wide-spread. Approximately 65–85% of plant pathogens are considered invasive [63]. Thus, there is a critical need for invasive pathogen ecology to elucidate the extent to which invasive pathogens harm natural systems. Based on our current understanding, it is unclear whether or not invasive fungal pathogens persist in the soil for years after invasive plants have been removed or whether these pathogens interact with other microbes in the soil to the detriment of native species. In other words, more research is needed to bridge the gap between plant pathology and ecology to better understand the impact of invasive pathogens in natural systems [1].

Introduction of non-native pathogens is one way invasive plants influence soil pathogen composition. However, they have also been shown to influence the abundance and diversity of native fungal pathogens in invaded sites, in ways that are often either beneficial [67] or detrimental to their growth. Alkaloids produced by these pathogens can inhibit generalist pathogenic fungi, which inadvertently stimulates the growth of host-specific pathogens [68]. This accumulation of pathogens specific to the invasive plant may actually allow native plants to thrive [69]. Some studies have shown that certain invasive grasses may produce chemicals which are said to have an inhibitory effect on competitors and may deter herbivory or either repel pathogens [25, 66]. In contrast, some invasive plants may release chemicals known to attract pathogens (Accumulation of Local Pathogens Hypothesis) [71], which could act as a "pathogen reservoir," leading to reduced competition by local plants [72].

3. Restoration efforts to reverse biotic changes

Plant communities are dependent upon soil microbial communities; therefore, native plant restorations may ultimately not be successful unless the microbial and plant communities are simultaneously restored. The idea of using microbes, either a component of the native-plant associated microbial community or an entire whole soil inoculum isolated from an intact ecosystem, as a biological control against the spread of invasive species has gained popularity in recent years.

Restoration ecologists are now applying AMF cultures [37], whole native soil, or biological crust to their restorations in hopes of augmenting native plant establishment (**Figure 5**). Addition of native soil to restoration sites has been found in some studies to decrease invasive plant cover and increase the native plant cover [73]. It

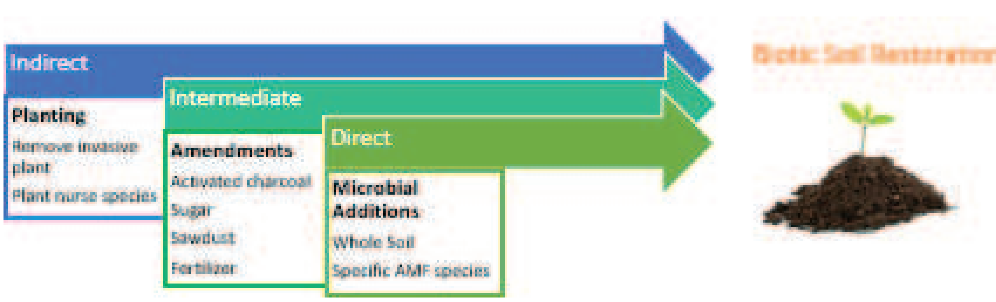

Figure 5.
Diagram showing the indirect, intermediate, and direct methods of biotic soil restoration. Indirect methods include removing invasive plants and planting nurse species. Intermediate methods include soil amendments such as activated charcoal, sugar, sawdust, and fertilizer. Direct methods include the addition of whole soil or specific AMF species to the soil.

is important to compare the methods of these types of studies to understand what inoculation method is most successful for combatting a particular invader [6, 69, 70]. Some studies, for example, remove the invasive plant before applying soil inoculum to restore soil fungal abundance [10] or combine fertilizer with the inoculum. Microbial soil inoculations have been found to actually inhibit the allelochemical effects of an invasive plant on a native plant species [75].

Other possible means of managing invasive plants at the microbial level include the addition of sugar, sawdust, or activated charcoal to soils. Sugar and sawdust can increase microbial growth and store excess soil nitrogen from invasive plants in the microbial biomass [76] (**Figure 5**). This method has been successful for some invasive sites, but not all [9]. Soil additions of activated carbon are believed to bind invasive plant allelochemicals and remove them from the soil solution [77]. Because allelochemicals are short-lived, this technique is most useful if the invasive plant is still present in a site [9]. Studies have shown that native plant growth increases with the addition of activated charcoal under invasion by spotted knapweed (*Centaurea maculosa*), diffuse knapweed (*Centaurea diffusa*), and cheatgrass (*Bromus tectorum*) [9]. Activated carbon can have numerous other effects on the soil (binding organic substrates, changing soil nitrogen concentration, and changing the carbon-to-nitrogen ratio), [9] so further research is needed to decouple these effects with the aforementioned binding of allelochemicals.

3.1 Restoration of arbuscular mycorrhizal fungi and ectomycorrhizal fungi

Invasion by non-mycorrhizal plants can sometimes reduce the abundance of AMF in the soil, negatively impacting native plants that are dependent on AMF for survival. A decrease in AMF abundance can encourage further invasion by non-mycorrhizal plants, thus maintaining invasive plant dominance and inhibiting native plant growth [78]. This is of special concern considering many other studies have found invasive species that are less dependent than native plants on AMF [12, 21, 73–75]. In situations where the invader is known to be non-mycorrhizal, restoration strategies that increase the soil AMF abundance could be especially effective combined with native plant seeding and planting AM host plants. AMF addition to soil has been useful in some restorations efforts [79], but not all [80]. In some cases, when an invaded site has sufficient AM propagule pressure, adding additional AMF may not have any effect on AM abundance or native plant performance [77]. Furthermore, a singular increase in AMF abundance may not be sufficient for restoring native plant diversity, but rather an increase in AMF diversity along with augmenting specialist AMF propagule pressure may improve restoration outcomes [22].

Although some land managers consider the co-invasion of ectomycorrhizal fungi to be a threat to native communities, as of yet there have been minimal evidence-based management strategies documented by practitioners [53]. Removal of plants that associate with ectomycorrhizal fungi, chemical sprays, and sporocarp removal have been performed, but the success of these strategies is debatable. Picking mushroom caps has been shown to have little impact on invasive fungal populations [81], but this may be because studies have focused mainly on fungi that are neither short-lived nor reproduce sexually [53]. Fungicide is another option, but it may also damage native fungi, thereby doing more harm than good to native plants.

3.2 Fungal pathogens and implications for restoration

Very few papers recommend restoration strategies for mitigating the effects of invasive pathogens [53] and even less recommend strategies for preventing the accumulation of pathogens by invasive plants. Most restoration strategies for combatting pathogens are primarily focused on agriculture, not natural systems, and those that do cover natural systems focus primarily on hardwood forests. Restoration of chestnut trees has been extensively studied in the wake of the aforementioned chestnut blight fungus.

Recommended strategies include planting blight resistant trees [82], creating strains of blight fungus that are less virulent [83], and crossbreeding trees [84], such as naturally resistant Asian chestnut trees and American chestnuts. Although many papers focus on gene manipulation as a restoration strategy, others suggest more large-scale strategies such as maintaining tree stand structure, maintaining healthy and resistant tree species, and timber extraction [85]. Some researchers recommend inoculating specific ectomycorrhizal fungi to boost the vigor of infected trees [86]. Blight fungus and hardwood tree infections could potentially be used to guide further research about ecological restoration in other natural systems ravaged by invasive pathogens.

The most successful strategy for combatting invasive fungi is to prevent them from being introduced in the first place. This could involve either banning plants that associate with known invasive fungi or by preventing nurseries from inoculating their plants with invasive fungi [52].

4. Conclusion

Arbuscular and ectomycorrhizal fungi play important roles in the nutrient acquisition and maintenance of biodiversity. Evidence concerning the impact of invasive plants on these fungal groups has been mixed, with AMF occasionally illustrating an increase in abundance [14, 28, 29], a decrease in abundance [39], or a shift from specialist to generalist AM taxa [3, 35]. These conflicting results underscores the importance of future research on the response of AMF to invasion and invasive plant management, with an emphasis on the role of factors driving their response, such as invasive plant functional group [35].

Although little is known about ECM, highlighting a need for future investigation, the evidence suggests that both non-mycorrhizal invasive plants [43–45] and allelopathic invasive plants [50] may inhibit their EM fungal growth, which may interfere with plant nutrient acquisition in both boreal and temperate forests. The introduction of harmful invasive ECM which facilitate in the co-invasion of trees may further disrupt forest symbioses [53].

Invasive plant encroachment into ecosystems have unintended consequences for microbial pathogens, such as influencing the abundance and diversity of native fungal pathogens in ways that benefit their growth or harm native plants. Indeed, invasive plants alter soil fungal composition [63, 67, 82]. The spread of invasive pathogens by invasive species has been widely covered in agricultural research. Future research should focus on invasive pathogens that are being transported by an invasive host plant to natural systems other than hardwood forests. A majority of studies focused on natural systems, emphasize primarily hardwood forests and the loss of foundation tree species. The loss of these foundation species has impacted nutrient fluxes, water movement, biodiversity, and food webs of infected forests [65]. These sorts of large-scale changes could have cascading effects that last for many generations.

Conflicting results and a lack of microbial data has led to case-dependent, anecdotal restoration recommendations. The results of inoculation experiments are very encouraging for improving restoration efforts. However, it may be particularly useful in the future to evaluate exactly how the microbial composition changes for each invasive plant, especially at the species level or for plant functional groups.

While more restoration ecologists are making decisions based on important microbial-plant mutualisms, much more information is needed concerning the long-term impact of invasion on fungi, especially mycorrhizal fungi and fungal pathogens.

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