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A Systematic Review of Terrestrial Plant Invasion Mechanisms Mediated by Microbes and Restoration Implications

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Abstract

Terrestrial invasive plant species continue to wreak havoc on a global economic and ecological scale. With the advent of climate change and pending future catastrophes, the spread of resilient invasive plants will only increase exponentially. Here, the search continues for a better understanding of the below-ground microbially driven mechanisms involved in plant invasion where other above-ground mechanisms have been exhausted. Microbes govern the world around us and interact with every living and non-living facet of the world. To reinforce the important underpinnings of the role of microorganisms in plant invasion, a systematic review of recently published articles was undertaken. Using the ScienceDirect database, five (5) search queries were used to generate 1221 research articles. After a two-step reduction was made based on relevance of the articles, a final total of 59 articles were retrieved. An additional 18 relevant articles were also assessed through the PubMed database for analysis to account for other invasive plants. Thirty-seven (37) invasive species were investigated where soil physiochemical and microbial community structure changes were most prevalent (32% & 39% respectively) while enhanced mutualism, allelopathy and pathogen accumulation were reported less (16%, 10% & 3% respectively). In all invasive species assessed, the impact on plant invasion and inability of the native plants to compete was due to specific microbial associations of the invasive plant or disruption of the soil microbial community. This microbial community shift coincided with changes in physiochemical properties of the soil and the subsequent negative soil feedback for native plants. There is still an expanding potential for the use of biocontrol agents to aid restoration once the underpinnings of biotic resistance and enemy release are understood in a microbial and physiochemical context. The active and functional microbial community structure of the invasive plant rhizosphere and adjacent soil in its native and non-native region can offer a better inference of how they can be controlled using novel-below ground biocontrol methods.

Keywords

Invasive Plant, Biotic Resistance, Biocontrol Agents, Enemy Release, Restoration

1. Introduction

The number of invasive plant species across the globe is astronomical. North America and Oceania have the highest prevalence of terrestrial invasive plant species (341) (**Figure 1**) with 1662 total invasive plants spread out across the major continents [1]. The high prevalence of invasive plants in higher income countries is mainly due to a constant up-tick in trade and transportation of goods as development progresses [2]. It is well known that exotic invasive plants contribute to disruption of economies, ecological structure and function of non-native regions in which they encroach [3]. Invasive plants have caused up to 40% of agricultural crop yield losses globally while displacing other native plant species [4]. Exotic invasive plants employ numerous classical mechanisms such as enemy-release, enhanced mutualism, novel weapons, allelopathy, pathogen accumulation to name a few [5] [6] [7] [8]. Most if not all these below-ground mechanisms of plant invasion have an effect on the soil microbial community, soil physiochemical and biogeochemical properties in the non-native invaded community [9] [10] [11] [12] [13]. All plants will indeed cause a disruption of the soil microbial community adjacent to its rhizosphere through plant exudate production influencing active recruitment and reduction of beneficial and antagonistic/pathogenic microorganisms respectively. Plants require essential nutrients from the soil such as P, N, Ca, Mg, Fe which may not be readily assimilated but available through recruitment of different microorganisms for which C exudates are produced by the plants in return. Many microorganisms in soil such as AMF/EMF, saprophytic and pathogenic fungi, N-cycling bacteria, sulfate reducers [14] [15] [16] [17] and others with yet to be discerned mechanisms influence the soil nutrient, physiochemical and biogeochemical profile. If these changes are of benefit to the plant, a positive-soil feedback effect will result, enabling the proliferation of that plant or in the opposite scenario, development of a more negative-soil feedback reducing plant success. Invasive plants tend to be more resilient to abiotic and biotic changes than native plants. Due to the genetic differences between plants, the chemical make-up of their exudates would be unique to each plant creating their own novel rhizosphere microbial communities. The microbial component of native and non-native soils plays an important role in plant success and inevitably plant invasion [11] [18].

Many, if not all invasive plants, are not considered as a nuisance in their native habitat but once introduced to a new non-native environment, and consequently overcoming the establishment stage, they spread almost uncontrollably, damaging these naïve ecosystems. The ease at which invasive plants overcome introduction and establishment is determined by abiotic and biotic factors in the non-native habitat [19]. This important determining factor of plant invasion is biotic resistance which is the reduction in invasive success by the native community through competition [19]. This factor is quite ubiquitous in North America and tropical/subtropical regions where environmental conditions are more favorable. Above-ground effects of biotic resistance are well seeded in literature [19] where high diversity of native plant species has mostly been effective in reducing establishment of invasive species. Poorly understood however, are the below-ground biotic factors [18]. It does however seem highly plausible that disruption of mycorrhizal and bacterial networks during disturbance, prolific exudate production by invasive plants, the lack of plant pathogens, herbivores and other insects in the non-native habitat contributes to lowered biotic resistance. The differences in soil microbial dynamics between the native and non-native habitat are also poorly understood when trying to understand invasion. To fully understand the role of microorganisms, this systematic review will focus on research articles where the prospective mechanism of plant invasion is delineated and the possible link between the mechanisms and members of the rhizosphere/adjacent soil under invasive plants which contribute to invasion are known. Studies employing next generation sequencing methods will be assessed in more detail since other older methods such as phospholipid fatty acid analysis (PFLA) give only a broad assessment of microbial community structure. This review will also investigate new strategies to assist with restoration of native populations and reduction of invasion.

2. Main Objectives

This systematic review article aims to assess globally, through the synthesis of 59+ research articles, the potential roles played by soil microorganisms during plant invasion. It also seeks to find the linkages between specific microbial associations in invasive plants or the shifts in microbial community structure and the inferred invasive mechanism. Lastly, it will identify potential solutions on the horizon for restoration of invaded sites through land management and soil microbiome engineering. We then determined the below specific objectives:

1) What is/are the most prevalent mechanism of plant invasion in tree and weedy species?

2) What roles do soil microorganisms play in relation to these different plant invasion mechanisms?

3) What land management and microbe engineering methods have been employed to reduce plant invasion or improve the success of native plants?

3. Methods

3.1. Study Area

In this review, terrestrial invasive plant species across six (6) continents were selected based on GISD descriptions and included: North America, South & Central America, Oceania (Australia), Africa, Europe and Asia (**Figure 1**). Most Caribbean islands, Russia, Middle East and other temperate regions were excluded as there were minimal research articles on invasive plants that fulfilled the criteria for selection.

3.2. Search Query

To search for relevant journal articles, ScienceDirect database was used with 5 search queries seen below and selecting research articles only, dated from 2006-2021.

1) "Invasive plant" AND "microbiome" AND "rhizosphere";

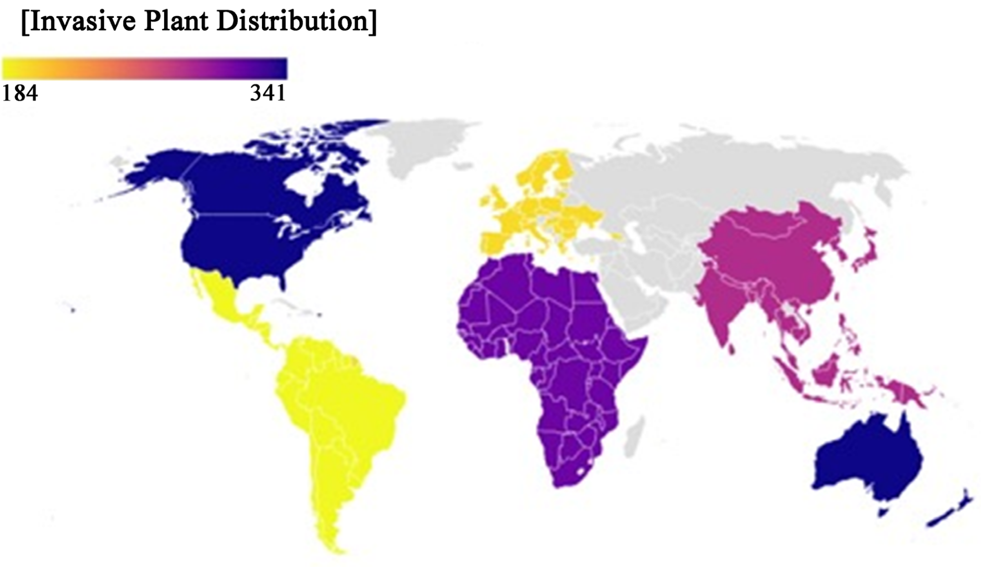
2) "Exotic plant" AND "mycorrhiza" AND "invasive" AND "native";

3) "Invasive plant" AND "restoration" AND "soil" AND "bacteria" AND "fungi";

4) "Invasive weed" AND "rhizosphere" AND "sequencing";

5) "Invasive shrub" AND "microbe" AND "soil".

A total of 1221 review articles were found from using the search queries, which was further narrowed down to 139 after reading the title and deciding if the topic was relevant to the specific objectives. Another round of reductions was made after reviewing the abstract and conclusions and removal of duplicated articles to produce 59 research articles (**Figure 2**). In addition to the search query which missed a few important invasive plants, additional search queries were used on the NCBI PubMed database for more articles that fulfilled the objectives. These additional search queries shown below as examples provided an



Data collected December 2,2021
Source:GSID·Created with Datawrapper

Figure 1. Current GISD (Global Invasive Species Distribution) of terrestrial invasive plant species across the different continents where North America and Australia exhibit the highest prevalence of plant invasion (341) and Central and South America having the lowest prevalence (184).

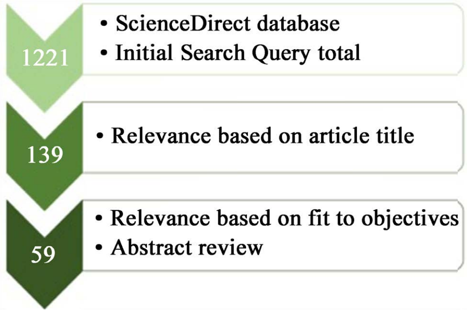


Figure 2. Gradual reduction of research articles relevant to the objectives of the systematic review from the above mentioned 5 search queries in the ScienceDirect database.

additional 18 articles used to also obtain background information on invasive plant mechanisms and a more recent update on the global status quo of invasive plants control.

“*Schinus terebinthifolius*” “invasion” “soil microbes”
“*Casuarina equisitifolia*” “invasion” “soil microbes”
“*Alliaria petiolata*” “invasion” “allelopathy”
“invasive plant” “restoration strategies” “microbes”

4. Results

4.1. Synthesis of Research Articles Based on Invasive Plant Mechanisms and Microbial Interactions

A total of 37 terrestial invasive plants were used in this review and includes some of the most invasive plant species across the globe, including *Alliaria petiolata* (garlic mustard), *Chromolaena odorata* (siam weed), *Solidago canadensis* (Canada goldenrod), *Ageratina adenophora* (Crofton weed), *Berberis thunbergii* (Japanese barberry) and *Schinus terebinthifolius* (Brazilian pepper tree). Out of these 37 species, 21 had known microbial associations in the rhizosphere while for 16 others the rhizosphere microbial community structure or key taxonomic groups have not been fully deciphered. The effect of these 16 species which lacked known plant-microbial associations were still important as the authors showed the effect of the plants on the adjacent or bulk soil environment. From these 37 species of invasive plants, the projected invasive mechanisms were grouped into 4 categories (Figure 3). Some invasive plant species had multiple projected invasive mechanisms (Table 1). Competition was not added as a possible mechanism as it is certain that all invasive plant species through these different mechanisms improve their competitive advantage against native plant species through a positive soil feedback effect.

4.2. Allelopathy & Allelochemical Production

A total of 7 of the 37 invasive plant species had reports of allelochemical production and/or allelopathic effects (3%)—Figure 3. The mostly studied invasive plant exhibiting this mechanism include *Alliaria petiolata, Impatiens glandulifera, Quercus rubra, Rosa rugrosa, Acacia dealbata, Schinus terebinthifolius* and

Table 1. List of select invasive plants across the world indicating their known/unknown microbial associations, invasive mechanisms along with their native and non-native regions.

Invasive plant	Microbe association	Possible Mechanism	Native Region	Non-Native region	Reference
Acacia dealbata (silver wattle)	Unknown	allelochemical production—soil bacteria community more affected	Australia	Portugal	[20]
Ageratina adenophora (crofton weed)	*Clostridium* + *Enterobacter* spp., *B. cereus*	Enhanced mutualism, increased Nitrogen metabolism, increased litter decomposition?	Mexico	China	[21] [22] [23]
Alliaria petiolata (garlic mustard)	Unknown	allelopathy, higher pH, higher N rates—affects resource availability, microbial community shift, plant fungal mutualism disruption (novel weapons)	Europe	North America	[9] [10] [24] [25]
Amaranthus retroflexus (red-root amaranth)	N-fixing bacteria	increases richness of N fixing bacteria to further success	South America	China	[26]
Amaranthus spinosus (spiny amaranth)	N-fixing bacteria	changes soil nitrogen fixing bacteria community structure	South America	China	[27]
Ambrosia artemisiifolia L. (annual ragweed)	sulfate reducing bacteria, Actinomycetes	Disruption of abiotic and biotic soil community, <pH, > soil organic C, >NPK	Central America	China	[28]
Berberis thunbergii DC. (japanese barberry)	Alphaproteobacteria Nitrospirales & Pseudomonadaceae	increase in N cycling	Japan	USA	[29]
Brassica nigra (black mustard)	Unknown	disrupts soil fungal mutualisms	North Africa	USA	[30]
Bromus tectorum (cheatgrass)	Bacteriodetes	disruption of soil microbial community	Europe	USA	[3] [31]
Carpobrotus edulis (sour fig)	Verrucomicrobia, Acidobacteria, Sphingomonadaceae	soil physiochemical and microbial community flux	South Africa	Spain	[32]
*Casuarina equisitifolia (*Australian pine)	*Frankia* spp.	soil nutrient flux, leaves have allelopathic properties	Australia	USA	[33]
Centaurea solstitialis (yellow starthistle)	Proteobacteria, Firmicutes, sulfate reducing bacteria	reduction in pathogen accumulation/diversity	Mediterranean basin	USA	[11] [34]
Chromolaena odorata (L.) (Siam weed)	*Fusarium semitectum*	decrease in microbial biomass in invaded soil, increase in organic C, N and P, soil pathogen accumulation	North & South America	West Africa	[6] [35]
Conyza canadensis (horseweed)	Actinobacteria, Sphingomonadaceae Glomeromycota,	self-promoting soil nutrient flux, microbial community structure shift—decreased fungal diversity	North & South America	China	[36]
Falcataria moluccana (Moluccan albizia)	Unknown	shift in microbial and biogeochemical community structure—decreased P, increased C and N	South Asia	USA	[37]

Continued

Flaveria bidentis (coastal plain yellowtop)	*Rhizophagus intraradices*	Enhanced competition/mutualism through AMF colonization	South America	China	[38]
Heracleum mantegazzianum (giant hogweed)	Unknown	Changes in soil chemical and biological characteristics	Central Asia	Czech Republic	[39]
Impatiens glandulifera (Himalayan balsam)	Unknown	allelochemical production (naphthoquinone)—disrupts ECM & AMF interactions with native plants, disrupts hyphal associations—increase in saprophytic fungi	Himalayas	Switzerland	[40] [41]
Kalanchoe daigremontiana (alligator plant)	Unknown	increases C and N mineralization	Madagascar	Venezuela	[42]
Lantana camara (West Indian lantana)	Unknown	increased nutrient cycling—C, N & P	North & South America	India	[43]
Melinis minutiflora (molasses grass)	Nitrifying bacteria	increase in N cycling	Africa	Brazil	[44]
Mikania micrantha (bitter vine)	P solubilizing bacteria—*Burkholderia* spp.	increased P in plant—enhanced mutualism, increased C accumulation and release to soil microbes	Central & South America	China	[45] [46]
Phragmites australis (common reed)	Unknown	increased nutrient availability in rhizosphere—positive plant feedback	Eastern Australia	Australia	[12]
Polygonum cuspidatum (Japanese knotweed)	Unknown	increased SOC, N deposition enhanced SOC accumulation	East Asia	USA	[47]
Pseudotsuga menziesii (douglas fir)	AMF Association	Enhanced mutualism effect, alters mycorrhizal community structure	North America	Argentina	[48] [49]
Quercus rubra (native red oak)	Unknown	allelochemical production (phenols) elicits microbial community structure shift, shift in soil physiochemical properties	North America	Poland	[13] [50]
Reynoutria japonica (Japanese knotweed)	Unknown	reduces AMF species richness and abundance	East Asia	Poland	[51]
Robinia pseudoacacia (black locust)	Unknown	shift in microbial community structure—increased nitrification and acidification, reduced biodiversity	USA	Italy	[52]
Rosa rugosa (beach rose)	AMF association	soil nutrient flux, >total N, C & P, decrease in Microbial biomass, high phenolic content (allelochemical)	Asia	Poland	[53]
Schinus terebinthifolius (brazilian pepper tree)	*Glomus* spp., Verrucomicrobia, Acidobacteria	shift in soil microbial community—decreased prevalence of soil fungal pathogens, allelopathy, competition	South America	USA	[16] [54] [55] [56]
S*olidago canadensis* (Canada goldenrod)	Nitrogen fixing bacteria, *Glomus geosporum*	increase soil N availability (enhanced mutualism hypothesis), reduction of *G. mosseae* prevalence required by natives	North America	China	[15] [57] [58]

Continued

Solidago gigantea (giant goldenrod)	Phosphate solubilizing bacteria	increased phosphorus mineralization	North America	China	[14]
Sorghum halepense (johnson grass)	Nitrogen fixing bacteria, *Pseudomonas* sp., *Caulobacter* sp., *Sphingobium* sp., *Agrobacterium tumefaciens*	alteration of biogeochemical cycles—N, C, P, Fe, IAA production	Asia/Northern Africa	USA	[17]
Spartina alterniflora (smooth cordgrass)	Unknown	microbial metabolism flux driven by pH and salinity, AMF colonization disruption	North America	China	[59] [60]
Thymus vulgaris L. (common thyme)	Unknown	shifts in soil physiochemical properties—decreased soil P, moisture	Southern Europe	New Zealand	[61]
Wedelia trilobata (trailing daisy)	Unknown	shift in soil biogeochemical properties, nitrogen cycling—pH, Ca, increase richness of fungal community	Central America	China	[62]

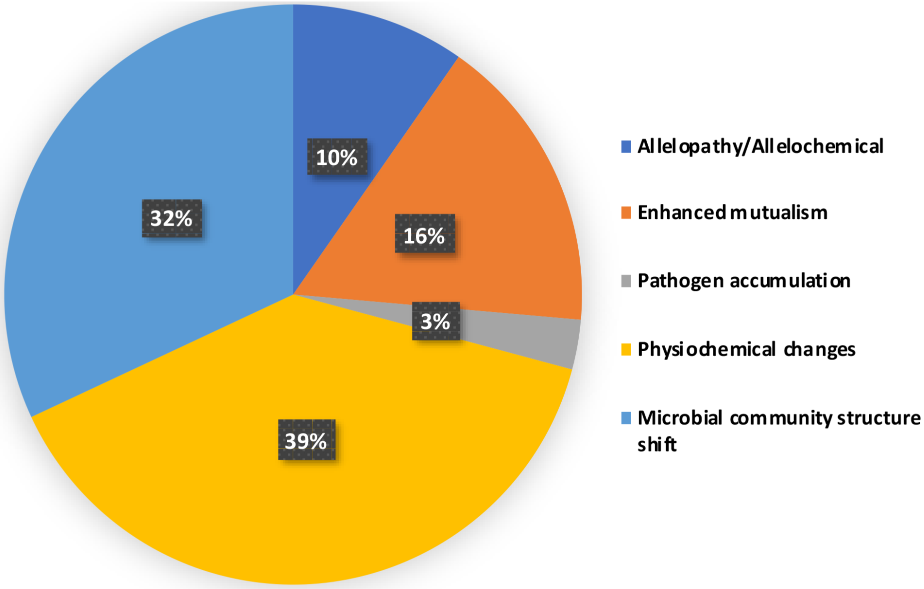


Figure 3. Distribution of plant invasion mechanism across the 37 species of invasive plants undertaken in this study.

Casuarina equisitifolia. The most widely studied model invasive plant for allelopathy is *Alliaria petiolata* where specific glucosinolates were isolated and found to be directly inhibitory to adjacent native plant species [10] [24]. Since this chemical is very unique, a novel weapons mechanism is also mentioned where the non-native habitat environment has no evolutionary history with this chemical. *Impatiens glandulifera* also produces a known allelochemical naphthoquinone which caused a disruption in fungal interactions with native plants [40] [41]. *Schinus* and *Casuarina* also exhibited similar effects but more so showing direct allelopathy of plant extract and leaf litter in inhibiting germination and succession of native plants [33] [56]. For all these plants, allelopathy/allelechemical production did not operate solely on its own but occurred in combination with other invasive mechanisms where there was a direct correlation between production and changes in the soil microbiome community and physiochemical characteristics of the soil.

4.3. Enhanced Mutualism

Enhanced mutualism of invasive plants was reported in 12 of the 37 species (16%). This mechanism could only be confirmed fully for plants where an investigation of specific taxa and their functional properties were assessed under the rhizosphere of the invasive plant. The most widely studied examples include *Ageratina adenophora* which was enriched with *Clostridium*, *Enterobacter* and *Bacillus cereus* which directly impacted its growth and competition against surrounding native plants [21] [22] [23]. *Berberis thunbergii* showed an increase in nitrifying bacteria and associated functional properties which shifted the microbial community structure adjacent to the plant [29]. Quite a few plants that exhibited enhanced mutualisms accomplished this by forming strong associations with arbuscular mycorrhizal fungi, *Frankia* spp. and phosphate solubilizing bacteria as seen for invasive plants such as *S. terebinthifolius, Conyza canadensis, Flaveria bidentis* and *Mikania micrantha [16]* [36] [38] [45] [46]

4.4. Pathogen Accumulation

Only two invasive species reported a significant impact of pathogen accumulation in the adjacent soil of the plants during invasion. These two species were *Chromoloena odorata* and to a lesser extent *Impatiens glandulifera*. *C. odorata* with its association with known fungal pathogen *Fusarium semitectum* increased over 2-fold the concentration of fungal spores in adjacent soil during invasion [6]. This led to a decrease in overall microbial mass and increases in soil nutrient level [35]. The rhizosphere microbial associations of *Impatiens glandulifera* are mostly unknown but it was shown to increase the prevalence of saprophytic and potentially pathogenic fungi during invasion [41].

4.5. Changes in Physiochemical Properties of Soil

This mechanism was the most widely reported, exhibited by 28 invasive plants (39%). Soil physiochemical changes go in tandem with microbial community structure shifts, allelochemical production and pathogen accumulation in over 70% of plants. It was seen mainly with plants such as *Casuarina, Berberis, Amaranthus* sp. and *Quercus* that harbored nitrogen fixing bacteria or had allelochemical production as an additional mechanism.

4.6. Soil Microbial Community Structure Shift

This was the second most prevalent mechanism (32%) exhibited by the invasive plant species. The impacts of soil microbial community shifts coincided with shifts in physiochemical properties of the soil, which was reported in plants such as *Sorghum halepense*, *Solidago canadensis*, *Rosa rugosa* and *Quercus rubra*. Both allelochemical/allelopathy and pathogen accumulation mechanisms described above involved microbial community structure shifts. Notably, it was shown that a shift in microbial community structure after increased invasion of horseweed which accumulated Actinobacteria, Sphingomonadaceae and mycorrhiza in its rhizosphere caused a soil nutrient flux [36]. These associations affected negative soil feedback for native plants while having positive-soil feedback for the invasive. In a similar pattern, Rodríguez-Caballero *et al.*, 2020 [32] showed that the invasive plant *Carpobrotus edulis* affects microbial community structure and soil physiochemical properties leading to negative soil feedback for native and positive soil feedback for the invasive.

4.7. Restoration Strategies Employed to Reduce Plant Invasions

Land managers continue to employ mainly above-ground methods of prescribed burning and herbicide treatments to control the spread of invasive plants. With the known significance and importance of the soil microbial community to invasion what has been shown in the literature to be effective based on the geographical and invasive plant context? Prescribed burning for one, even though it mainly affects the above ground biota, also can affect the below ground microbial community in a significant way. Burning creates a somewhat "sterile" environment with reduced activity of mycorrhiza, bacteria and lowered nutrient levels. It was shown that one native plant was able to out-compete an invasive plant in the burnt (sterilized) soil [63]. In another indirect way, the use of a parasitic climbing plant *Cuscata australis* shifted the rhizosphere microbial community under the invasive plant *Alternanthera philoxeroides* improving the success of nearby native plants [64]. This novel method is one of the first employing the use of natural enemy parasitic plants in controlling invasive plants.

Invasive plants through the disruption of the soil microbial community which in turn affects the biogeochemical and physiochemical properties of the soil can have long term effects, even after their removal. This legacy effect [55] can be restored by the use of microbial inoculants [65]. This microbial inoculant which includes beneficial bacteria, mycorrhiza and other fungi was shown to improve native seedling performance in the presence of invasive plants. Another unique study employed the use of weed-suppressive bacteria (*Pseudomonas fluorescens*) to reduce the invasive effect of downy brome (*Bromus tectorum* L.), jointed goatgrass (*Aegilops cylindrica* L.) and medusa head (*Taeniatherum caput-medusae* L.) [66]. One of the most compelling findings involved the transfer of pathogens from the native plant region to the non-native region where the same plant is now invasive. This was reported for *Euphorbia* spp. (leafy spurge) where the most virulent pathogens associated with the native plant (*Fusarium* + *Rhizoctonia* sp.) where isolated and used as biocontrol agents to stem invasion in the non-native range [67].

There is some caution however to the use of microbial inoculants, as due to the specificity of interactions some of these microorganisms with plants, they may not have the same effect in different geographical locations and soil with varied nutrient levels and physiochemical properties. In one study, it was shown that inoculation of plant growth promoting bacteria influenced the proliferation of invasive *A. adenophora* over other native plants [68]. [69] Dai *et al.*, 2016 also reported that addition of PGP endophytic bacteria such as *Bacillus* sp. improved the growth of the invasive plant *Wedelia trilobata* over the native congener.

5. Discussion

Biotic resistance of soil is the key element in the determination of a plant becoming invasive [19]. If there is a significant difference in the soil biota and abiotic factors in the native vs non-native region this will more than likely cause a reduction in biotic resistance and consequently establishment and spread of the newly invasive plant. These reports [21] [67] gave some credence to the importance of the enemy release hypothesis for invasive plants. Enemy release and biotic resistance in a soil microbial community context have the greatest potential for understanding why plants native in one geographic location become invasive in another location. [67] showed that the soil pathogens which have been evolutionarily adapted to the plant in the native region are missing or of low prevalence in the non-native region where the plant becomes invasive. But by transferring the native soil pathogens to the non-native region, there was a reduction in the succession of the invasive plant. Similarly, the use of pathogens and other non-mycorrhizal microorganisms from native congeners which have the ability to reduce plant invasion or increase biotic resistance in the non-native range was shown for invasive plants *M. micrantha* and *E. catarium* [21]. The lack of a highly diverse soil pathogen community negatively affects the ability of the non-native ecosystem to reduce the establishment of the invasive plant, which is tied into a low biotic resistance effect. Both these mechanisms are influenced by the soil microbial community.

The impact of the soil microbial community during plant invasion is normally at the center of all the different invasive mechanisms. It is still difficult however to determine if the changes in microbial communities are driven by direct plant microbial interactions or as a result of plant-driven changes in soil properties [70]. This is compounded by the fact that the pathogen accumulation effect for *C. odorata* was eliminated by sterile soil treatments and application of activated carbon removing the microbial and possible physiochemical effects of its invasion [6] [10]. Two research authors [10] [71] showed that soil biota might be involved in the deactivation of allelochemicals released by the invasive *A. petiolata* and *Eupatorium adenophorum* respectively. Another factor indirectly influencing allelochemicals fate in soil can be related to the quality and quantity of soil organic matter which usually increases during invasion.

In two studies supporting the importance of soil microbes, *Flaveria bidentis* and *Pseudotsuga menziesii* invasion through enhanced mutualism with AMF species led to a subsequent shift in the soil microbial community structure and negative soil feedback for adjacent native plants [38] [48]. A similar effect was observed for the invasive plant *R. rugosa*, which formed specific AMF associations while producing allelochemicals in the soil, constructed its own niche environment to improve its positive soil feedback at the detriment of native plants [53]. The effect of invasive plants on important native mycorrhiza community structure was evident in reports involving *S. terebinthifolius* and *S. canadensis* [15] [16]. More so for *S. canadensis* there was a direct link between the increase in composition of one Glomus species and depletion of another that lead to positive feedback for the invasive plant and a more negative feedback for the native plant. These microbial associations with invasive plants either directly or indirectly promote positive soil feedback loops and increased competition and dominance in relation to native plant species.

Two studies, however, had limited support for the role of microorganisms in plant invasion. One reported no significant change in microbial and eukaryotic communities in the invaded and native range for *Solidago* spp. [72]. Their taxonomic analyses were limited as they didn't fully tease apart the different taxonomic levels and reported mainly at the phylum and class level where significant changes may not be seen. For the invasive *Acacia* spp. soil fungal communities were similar in the invaded and native range and showed no effect on the success or failure of the invasive plant [73]. Again, a thorough analysis of the rhizosphere of the plants in both regions was not undertaken and the authors reported a major limitation in the type of primer used which may have detected a low diversity of species.

Invasive plants invest more resources in biomass allocation than defensive allocation in the non-native range, making them more competitive than native species. In their native habitat, there is a balancing act in allocating resources for defense from pathogens and recruitment of beneficial microbes. This balancing act causes a negative to neutral and possibly slightly positive soil feedback of plants in native habitat. There is also a longer evolutionary history of the native plants and soil pathogens where there is a constant ecological pressure that resists their proliferation and spread from becoming invasive. In controlling invasive plants, it is essential that a thorough analysis of the microbial community structure of the invaded and native region is undertaken using next generation sequencing methods, not only to know which taxa are present but those who play an active and functional role. If the microbial elements involved in enemy release and biotic resistance are fully understood, new biocontrol agents can be employed as an adjacent strategy for the eradication of invasive plants and restoration of invaded areas.

6. Authors' Contributions

KD put together the manuscript along with the analysis of the different journal articles. JM and OS helped with sourcing the different articles and review. NE also helped with the final review of the article.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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