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Role and influence of soil microbial communities on plant invasion

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Abstract. It is known that plant invasions are of major concern as they result in loss of biodiversity and alterations in ecosystem processes and functions. Although numerous mechanisms have been postulated to find out the reasons behind plant invasiveness, the actual and precise mechanism is still obscure. Soil microbes are considered as one of the important determinants of plant growth and establishment. Plant invasion leads to changes in the composition and structure of soil microorganisms. Most of the earlier studies have focused on the aboveground mechanisms of plant invasion. Recently the belowground mechanisms for plant invasion are being investigated. In this review, we focus on the various hypotheses related to soil microbes in either enhancing or suppressing plant invasions. The interactions between soil microbes with native and non-native plant species, the role of the plant-soil feedback system in the invasion and its impact, the function of mycorrhizal and bacterial symbiosis in plant species invasion and the role of soil biota and changes brought about in soil nutrient cycling and soil enzymes due to plant invasion are also discussed.

Key words: soil microorganisms, invasive plant, plant-soil feedback, mycorrhizal fungi, soil enzymes, soil nutrients.

1. Introduction

Some plants are introduced into an alien environment either naturally or deliberately where they proliferate and establish successfully. It has been estimated that around 13,000 plant species are growing outside their native range creating their own populations (van Kleunen et al., 2015). A species becomes locally dominant when introduced into a small area proliferates rapidly (Levine et al., 2003) and transforms the multispecies communities into mono-dominant ones. The plant species that alter the natural plant communities are commonly termed as invasive plant species (Colautti & MacIsaac, 2004). Nevertheless, the factors responsible for plant invasion are still being a primary challenge in the field of ecology. Generally, biological invasion is of major concern as it causes global environmental changes; alter the structure and function of ecosystems, biodiversity loss and also the extinction of species (Davis et al., 2000; Ogle et al., 2003; Mooney & Cleland, 2001; Vilà et al., 2007). The biogeochemical cycling of nutrients that are influenced by the plant species compositions is also altered due to plant invasion (Herr et al., 2007). The spread of alien plant species depends directly or indirectly on anthropogenic activities (Panetta & Scanlan, 1995) like trading and travelling across the globe by ships and aircrafts (Moore, 2004). Invasive plant species have the potential to colonize over an extensive area (Richardson et al., 2000) and can affect both, the human economy and health (Mack, 2001). An analysis of the available information on invasive plant biology suggests that biological traits of the invading plant species, the environmental conditions of the invaded ecosystem and their interactions with the native plant community play a key role in the successful establishment of the invasive plant species (Kolar & Lodge, 2001). Alien plant species are generally strong competitors than indigenous plant species (Blossey & Notzold, 1995; Vilà & Weiner, 2004) and compete directly with native plant species for the various resources (Werner et al., 2010).

Soil microorganisms (microbes) residing in the rhizosphere of plants are involved in several important processes. Soil microorganisms, mostly mycorrhizal fungi and bacteria affect the diversity and abundance of belowground soil organisms and thus can be substantial in response to plant invasion (Broz et al., 2007; Scharfy et al., 2010). The compositions of soil microbial community of invasive plants are different and have altered ecosystem functions from those of native plant species (Ehrenfeld, 2003). Numerous studies have shown that soil microbes are one of the key components that either facilitate or inhibit plant invasion (Bever, 2003; Inderjit & van der Putten, 2010; van der Putten et al., 2013; Inderjit & Cahill, 2015). Therefore, knowledge on the interactions between soil microbes and exotic invasive plant species provide a better understanding of the ecological roles of the soil biota functioning both at root-soil and root interface (Rout & Callaway, 2012).

Most of the previous studies indicate that plant invasion could alter the physiochemical properties of the soil (Rout & Chrzanowski, 2009; Novoa et al., 2014; Kuebbing et al., 2014). Among the different soil physiochemical characteristics, soil temperature, moisture, and pH are considered as the important factors in litter decomposition, soil nitrogen contents, metabolic activities and community structure of soil microbes (Wang et al., 2011). For instance, soil moisture and temperature increases following the invasion by *Acacia saligna* (Labill.) Wendl. (Yelenik et al., 2004). Plant invasion also increases soil pH (Kuebbing et al., 2014), but in certain cases, a low or high degree of plant invasion may increase or decrease soil pH levels (Si et al., 2013). A decrease in pH could lead to the higher solubility of nutrients like phosphorus in the soil. This may, in turn, promote plant invasion (Herr et al., 2007). These clearly indicate that plant invasion induces alterations in the physiochemical properties of soil. In this review, we focus on the interactions of invasive plant species with soil microbes, its feedback system, and the influence of exotic plant species on soil enzymes; nutrients and the role of soil biota in plant invasibility.

Most of the research on plant invasion has focused on the aboveground (Levine et al., 2003; Zou et al., 2008) than on the role of belowground mechanisms (Wolfe & Klironomos, 2005). Several mechanisms have been proposed to explain the role of soil microorganisms in plant invasion. Some of the hypotheses that relate soil microbes to plant invasion are enemy release hypothesis, mutualism hypothesis, enhanced mutualism hypothesis, degraded mutualism hypothesis, accumulation of local pathogen hypothesis and novel weapon hypothesis. One of the most pronounced mechanisms is the enemy release hypothesis that states the absence of antagonists during colonization resulting in the successful establishment of invaded plant species (Keane & Crawley, 2002; Blumenthal, 2009). *Hypericum perforatum* L., native to Europe, the western part of Asia and northern part of Africa, experienced reduced herbivores in its exotic range than in its native range (Vilà et al., 2005). Similarly, in *Ammophila arenaria* (L.) Link. invaded regions, the pathogenic nematodes were less abundant than its native regions (Beckstead & Parker, 2003). Liu and Stiling (2006) in a meta-analysis showed that about fifteen invasive plant species harbored the lower number of phytophagous insect species in their invaded regions than their native regions.

Accumulation of local pathogen hypothesis (Eppinga et al., 2006; Mangla et al., 2008) suggests that invasive alien plant species gather native soil pathogen that restricts native plant spread and growth. For example, the local pathogens accumulated by *A. arenaria* invaded soil decreased the growth and performance of native plant species by creating a negative effect on them (Eppinga et al., 2006).

The Novel weapon hypothesis postulates that invasive plants possess new biochemical weapons that function as strong allelopathic agents for new plant-soil-microbial interactions (Callaway & Ridenour, 2004; Callaway et al., 2008) and plant-soil feedback systems (Kardol et al., 2006; Kulmatiski & Kardol, 2008; Barto et al., 2010). *Alliaria petiolata* (M. Bieb.) Cavara & Grande in its introduced region in North America suppressed the growth and performance of native plant species by interrupting and decreasing the mycorrhizal fungal mutualists of native plant species through the production of new biochemicals. In contrast, *A. petiolata* in its native range failed to exhibit any inhibitory effect on mycorrhizal fungi (Callaway et al., 2008). The study on phytochemicals produced by *A. petiolata* that suppressed the performance of native plant species further supports the novel weapon hypothesis (Barto et al., 2010).

According to the enhanced mutualism hypothesis, some invasive plant species have a better association with soil mutualists in its introduced ranges than its native ranges that lead to successful invasion (Reinhart & Callaway, 2006). The degraded mutualism hypothesis states that invasion of an area by non-mycorrhizal plant reduces the abundance of arbuscular mycorrhizal (AM) fungi. Populations of *H. perforatum* introduced into North America were less dependent on AM fungi than the European, native populations. The reduced mycorrhizal dependence was related with finer root architecture compared to the root structure of the plant in the native range (Seifert et al., 2009).

2. Interactions between soil biota and invasive plants

It is important to elucidate how plant-soil interactions may cause evolutionary changes in invasive alien plant species to understand the role of environmental and plant traits differences in the successful establishment of invasive plant species (Mitchell et al., 2006). Numerous soil microbes have been isolated from invasive plant species (Table 1). Soil biota can influence the alien plant invasion through direct and indirect mechanisms (Reinhart & Callaway, 2006; van der Putten et al., 2007). Assessment of shifts in the microbial communities and their subsequent influence on the competition between native and invasive plant species could provide a better understanding of post-invasion changes (Hawkes et al., 2005; Zhang et al., 2010). Several studies on plant-soil interactions strongly suggest that introduction of exotic plant species has the potential to alter the microbial structure, function and chemical components of the soil. For example, Kourtev et al. (2002) studied the microbial communities of the rhizosphere and bulk soil of two exotic plant species, *Berberis thunbergii* DC., and *Micrstegium vimineum* (Trin.) A. Camus., and the native *Vaccinium* species and found variation in the structure and function of microbial communities in all the three species.

The interaction between microorganisms and plants can vary from mutualism to parasitism. In mutualism, both plants and the associated microbes benefit each other, whereas parasitism is a non-mutual relationship between species, where microorganisms, the parasite, lives at the expense of the plant host (Neuhauser & Fargione, 2004). Plant-soil microbial interactions of invasive plants differ from their native and non-native ranges (Callaway et al., 2004; Li et al., 2013). For instance, the soil microbial communities of *B. thunbergii* in its native regions differ from its invaded regions (Coats, 2014). Plants selectively influence the rhizosphere microbiota and establish feedback interactions between them (Kardol et al., 2007). Among all the soil biota, most of the terrestrial plants form a symbiotic association with the soil mycorrhizal fungi. Though mycorrhizal associations are usually presumed to be mutualistic, the nature of the association can range from mutualism to parasitism depending upon the plant species and environmental conditions (Johnson et al., 1997; Neuhauser & Fargione, 2004). Invasive plants generally promote the favorable soil microbes by establishing positive feedback (Batten et al., 2006; Sanon et al., 2011) and suppress the harmful ones (Lorenzo et al., 2010). The invasion of *Acacia dealbata* Link reduced the abundance of soil bacteria and fungi (Lorenzo et al., 2010). Yang et al. (2014) showed that invasive plant, *Solidago canadensis* L. affect the composition of mycorrhizal fungi by promoting the beneficial AM fungi and suppressing the detrimental ones. An invasive plant species modifies soil microbes in such a way that results in a positive or negative feedback effect (Bever et al., 1997; Suding et al., 2013). Among 201 invasive plant interactions investigated, 39.8% showed negative and only 18.9% exhibited positive feedback interactions (Kuebbing & Nuñez, 2014). Invasive plant species not only interrupts the long-term coevolved interactions among the native plants, but also the native plant-microorganism association (Callaway et al., 2008; Zhang et al., 2010). Changes in the composition of AM fungi were observed over two growing seasons in *S. canadensis* invaded regions (Zhang et al., 2010). These feedback processes may, in turn, affect the ecological processes, species interactions and temporal dynamics of plant communities (Reinhart & Callaway, 2006). The bacteria, fungi, actinomycetes and other rhizosphere mutualists involved in these interactions include mostly parasites or pathogens (Mitchell & Power, 2003), mutualists and symbionts (reviewed by Pringle et al., 2009) and saprophytes or decomposers (Allison & Vitousek, 2004).

The influence of nematodes feeding on an invasive grass *A arenaria* showed that plant roots were colonized by feeding generalist and not by feeding specialist in the non-native regions (van der Putten et al., 2005). The invasive soil pathogens that affect the natural vegetation have been mostly reported from the forest and ornamental plants. The soil-borne pathogen, *Phytophthora cinnamomi* Rands that causes root rot and mortality of plant species is considered as one of the most dreadful invaders all over the world (Garbelotto et al., 2006; Reinhart et al., 2010). *Prunus serotina* Ehrh., is suppressed by soil pathogen in its native region when compared to its non-native regions (Packer & Clay, 2000; Reinhart et al., 2003). Similarly, high incidence of native soil borne pathogen *Fusarium semitectum* Berk. & Ravenel was observed in the rhizospheric soil of an invasive weed *Chromolaena odarata* (L.) R.M. King & H. Rob., suppressed the native plant species (Mangla et al., 2008). Nevertheless, the same plant failed to harbour local soil-borne pathogens in an invaded alien area in South Africa (Te Beest et al., 2009). In a recent study pathogenic fungi associated with the roots of an invasive plant species, *Vincetoxicum rossicum* (Kleopov) Barbarich., were isolated from a highly invaded region and their effect on the growth of both non-native and two co-occurring native plants species were analyzed. The results of the study indicated that the pathogenic fungi increased the growth of *V. rossicum* but their effect on native plant species varied. These results suggest that the fungi colonizing the roots may be beneficial for the invading species and detrimental or pathogenic to the native plant species (Dai et al., 2016).

Mutualistic effects of soil microbes are considered as one of the important factors in determining plant invasiveness. Mutualistic microbes modify plant communities by either facilitating or inhibiting plant invasions depending

Table 1. Soil microbes isolated from the native and non-native regions of the invasive plant species

Invasive plant Species	Native regions	Invaded regions	Samples	Class/Group	Microbes isolated	Reference
Acacia mearnsii De Wild.	Australia	Brazil, Afghanistan, China, India, Indonesia, Srilanka	Rhizosphere	Proteobacteria	*Bradyrhizobium* sp., *Bradyrhizobium japonicum*	Le Roux et al. (2016)
Ageratina adenophora (Spreng.) R.M. King & H. Rob.	Central America	China, India	Rhizosphere	Actinobacteria	*Arthrobacter* sp.	Zhang et al. (2012)
				Proteobacteria	*Burkholderia* sp., *Rhizobium* sp., *Mitsuaria* sp., *Sinorhizobium sp.,* *Pseudomonas sp.*	
				Firmicutes	*Bacillus subtilis,* *Bacillus megaterium,* *Bacillus licheniformis,*	Niu et al. (2007)
				Proteobacteria	*Pseudomonas putida*	
Chromolaena odorata (L.) R.M. King & H. Rob.	Central and South America	Asia, Africa, parts of Australia	Rhizosphere	Fungi	*Fusarium semitectum*	Mangla et al. (2008)
					Botryosphaeria sp.	Xiao et al. (2014)
Lantana camara L.	Tropical America	Worldwide	Rhizosphere	Actinobacteria	*Kibdelosporangium lantanae* sp.	Li et al. (2015)
Mimosa acutistipula Benth. *Mimosa bimucronata* (DC.) Kuntze *Mimosa caesalpiniifolia* Benth. *Mimosa camporum* Benth. *Mimosa flocculosa* Bukart. *Mimosa pellita* Willd.	Central America	Australia, Taiwan, many African counties	Root nodules	Proteobacteria	*Burkholderia* sp.	Chen et al. (2005b)

Mimosa pudica L.	Central America	Australia, Taiwan, South Africa	Root nodules	Proteobacteria	*Cupriavidus tiawanensis* *Sinorhizobium* sp.	Chen et al. (2001, 2003a, 2005a)
Parthenium hysterophorus L.	North and South America, West Indies	Africa, India, Australia	Rhizosphere	Fungi	*Aspergillus niger,* *Aspergillus flavus,* *Aspergillus fumigatus,* *Chaetomium globosum,* *Eurotium chevelari,* *Curvularia lunata,* *Corynespora cassicola,* *Fusarium oxysporum,* *Fusarium moniliforme,* *Rhizopus stolonifer,* *Trichoderma harzianum*	Jeyalakshmi et al. (2011)
			Rhizosphere	Phosphate solubilizing bacteria	*Bacillus subtilis*	Dugar et al. (2013)
Robina pseudoacacia L.	North America	Asia, China, Europe	Root nodules	Symbiotic Proteobacteria	*Mesorhizobium robiniae*	Zhou et al. (2010)
				Symbiotic Proteobacteria	*Sinorhizobium* sp. *Rhizobium* sp. *Bradyrhizobium* sp.	Wei et al. (2009)
Sorghum halepense (L.) Pers.	Mediteranean regions	Europe, Middle East	Rhizome	Proteobacteria	*Sphingobium amiense*	Rout and Chrzanowski (2009)

upon the symbiotic interactions in native and non-native habitats (Hawkes et al., 2005; Richandson et al., 2000; Coats & Rumpho, 2014). The majority of the plants form the symbiotic association with AM fungi (Allen, 1991; Smith & Read, 2008), nitrogen fixing bacteria (Richardson et al., 2000; Ehrenfled, 2003) and with the wide range of other endophytes (Shipunov et al., 2008; Newcombe et al., 2009). Callaway et al. (2011) studied the impact of soil biota of an invasive tree, *Robinia pseudoacacia* L., from native, expanded and invasive ranges on nodulation and the nitrogen fixation and found the absence of mutualist and nitrogen fixing organisms in the invaded and expanded soil. In contrast, *R. pseudoacacia* formed nodules with nitrogen fixing bacteria in the native soil. The interactions between nonmycorrhizal fungal endophytes and the AM fungi are known to enhance plant invasiveness (Larimer et al., 2010). Bacterial endophytes help invasive plants by providing a higher amount of phosphorous and iron and also secretes plant growth promoting hormones (IAA), thus increasing the competitive ability of the invasive plants (Rout et al., 2013).

3. Soil biota and Plant Feedback System

Plants can modify the nature of the soil structure and chemical characteristics that in turn influence the plant's performance. This is usually referred to as plant-soil feedback (PSF) (Kulmatiski et al., 2008). The PSF is well-known invasion mechanism that operates in a natural system. As already mentioned, PSF can be either positive or negative. The positive feedback is favored mostly by mycorrhizal fungi, nitrogen fixing bacteria and beneficial soil microbes (Allen & Allen, 1984) and negative feedback are mediated by soil-borne pathogens, herbivores, and parasites (van der Putten, 2001). Soil biota exerts different impacts on native and invasive ranges (Inderjit & van der Putten, 2010). Positive feedback promotes intraspecific competition and predominance of plants due to the presence of symbiotic mutualists that enhance plant growth thus, also increasing interspecific competition (Bever, 2003). However, the negative feedback regulates and maintains not only the plant abundance but also the coexistence of other plant species (van der Putten et al., 1993; Mangan et al., 2010). The soil biota associating with *Centaurea maculosa* Lam., have greater negative effects on the plant growth when grown on native European soils in the absence of competitor. But, the soil biota that developed in association with *C. maculosa* in the non-native region (North American soil) showed highly positive effects on *C. maculosa*. Thus soil biota associated with native plant species can enhance the growth of exotic plant through positive feedback effect (Callaway et al., 2004). Similarly, assessment of PSF effect of 61 plant species (invasive, native dominant and native rare) in Canadian grassland and meadows suggested that native rare plants had negative feedback and invasive plants were benefitted from the liberation of soil-borne enemies thus exerting positive feedback (Klironomos, 2002).

An investigation on plant-soil biota feedback of 10 congeneric pairs of native and non-native herbaceous plant species showed more significant negative soil microbial feedback for native plant species when compared to non-native plant species (Agrawal et al., 2005). A comparison between native and non-native soils suggests that the native soil had a more suppressive effect on certain invasive plant species (Maron et al., 2014). Nevertheless, invasive plant species when introduced into a new area leave back the components that suppress the soil biota. AM fungi take part in plant-soil feedback between invasive shrub and native forest understorey species shrub and the woody invasive species change the AM fungal association of native plant (Shannon et al., 2014). The plant-soil interaction of an invasive species *Triadica sebifera* (L.) Small in its native and an invaded region showed that *T. sebifera* had a negative effect in its native range but always had a positive effect on invaded soil range (Yang et al., 2013), which favors the enemy release hypothesis.

Most of the studies examining plant-soil microorganisms feedback have proved that native plant species often experience negative soil feedbacks (Andonian et al., 2011; Reinhart et al., 2010). A meta-analysis showed that invasive exotic plant species suffer less from negative soil-feedback effect than the native plant species (Kulmatiski et al., 2008). In a greenhouse study, Niu et al. (2007a, b) examined the influence of an invasive plant species, *Ageratina adenophora* (Spreng.) King & H. Rob., and three native plant species on soil biota. The results of the study indicate that the soil biota linked with native species had a positive effect on the invasive *A. adenophora* and negative effect on native plants. Similarly, a positive feedback was also noticed in the invaded region for black cherry (*P. serotina*) to soil microbial communities and negative feedback in the native region (Reinhart et al., 2003). *Acacia delbata* Link invasion negatively affected the soil fungi and bacteria (Lorenzo et al., 2010). The effect of different species of AM fungi on plant-fungal feedback in serpentine grassland was studied. Among seven AM fungal species (*Glomus* sp. 1, *Rhizophagus intraradices* (N.C. Schenck & G.S. Sm.) C. Walker & A. Schuessler, *Glomus microcarpum* Tul. & C. Tul., *Gigaspora gigantea* (Nicol. & Gerd.) Gerd. & Trappe, *Claroideoglomus etunicatum* (W.N. Becker & Gerd.) C. Walker & A. Schuessler, *Scutellospora calospora* (Nicol. & Gerd.) C. Walker & F.E. Sanders and *Rhizophagus fasciculatus* (Thaxt.) C. Walker & A. Schuessler isolated from field soil and trap cultures, only *C. microcarpum* and *C. etunicatum* exerted negative feedback response on the growth of their particular hosts (Castelli & Casper, 2003). Species richness and soil context are important in determining PSF system. The changes caused by the invasive grass *Aegilops triuncialis* L., on the soil microbial populations had a negative effect on two non-native plant species grown in greenhouse conditions (Batten et al., 2008). The performance of the two native plants, *Lasthenia californica* DC. ex Lindl., and *Plantago erecta* E. Morris-remained unaffected in both native and invaded soil under field experiment thus leading to positive feedback in certain cases (Batten et al., 2006).

4. Role of mycorrhizal symbiosis in plant invasion

Mycorrhizal symbiosis is regarded as one of the key biotic interactions in the biosphere (Mummey & Rillig, 2006). Soil mutualist favors some of the plant invasions and few of the invasive plant species modify the soil-borne mutualists thus changing the native plant communities (Richardson et al., 2000; Callaway et al., 2008). Invasive exotic plant species also rely on soil microbes and AM fungi for mutualistic facilitation like the native plant species (Richardson et al., 2000). For example, the success of certain plant species like *Acer negundo* L., *Acer platanoides* L., *Bidens pilosa* L., and *Solidago canadensis* L., in their invaded region, has been attributed to their symbiotic association with mycorrhizal fungi (Reinhart & Callaway, 2004; Cui & He, 2009; Sun & He, 2010). Similarly, *C. maculosa*, an invasive plant species of North America invaded successfully through mycorrhizal mycelia network in its introduced range (Marler et al., 1999) and the competitive advantage of *C. maculosa* on the resident grass *Festuca idahoensis* Elmer are mediated by AM fungi (Zabinski et al., 2002). Inoculation of AM fungal species (*Rhizophagus irregularis* (Blaszk., Wubet, Renker & Buscot) C. Walker & A. Schuessler, *Funneliformis mosseae* (T.H. Nicolson & Gerd.) C. Walker & A. Schuessler and *Claroideoglomus claroideum* (N.C. Schenck & G.S. Sm.) C. Walker & A. Schuessler enhanced the growth, phosphorous concentration in roots and shoots of two invasive plant species, *Rudbeckia laciniata* L. and *Solidago gigantea* Aiton. (Majewska et al., 2017). Invasive plant species escape from their native enemies by altering the mycorrhizal association and competitive interaction with the native plant species in their introduced range (Shah & Reshi, 2007; Shah et al., 2008). The facultative mycorrhizal dependence of *Bromus tectorum* L. has to lead to the successful invasion of this plant species in American sagebrush steppe (Goodwin, 1992). Mycorrhizal mutualists are known to determine the patterns of invasiveness and abundance of few plant species (Levine et al., 2004). Invasive plant species that propagate and proliferate with less mycorrhizal dependency might reduce the AM fungal density in soil (Vogelsang et al., 2004). But in some cases, non-mycorrhizal invasive plant species have proliferated with elevated AM fungal density in the ecosystems (Stinson et al., 2006). The alterations in AM fungal abundance and species richness caused due to exotic plant invasions can either be unfavorable to the native plant species (Shah et al., 2008).

The changes induced in the mycorrhizal fungal communities results in a positive feedback cycle which in turn enhance the plant invasibility (Sun & He, 2010). Plant invasion may be inhibited due to changes in mycorrhizal fungal community composition (Pringle et al., 2009). When native [*Nassella pulchra* (Hitchc.) Barkworth, *Lupinus bicolor* Lindl.] and invasive plant species *Avena barbata* Pott ex Link and *Bromus hordeaceus* L., were grown together, the AM fungal community composition was altered (Hawkes et al., 2005). A meta-analysis on AM fungal interactions between native and nonnative plant species suggested that invasions fail to select the direction of shift. This does not support the divergent hypothesis that states plant invasion either promote or decrease the mutualistic association between plants and AM fungi. Though the abundance of AM fungi in both, native and invasive plant species did not differ, the AM colonization was lower in the native plant species when compared with invasive ones (Bunn et al., 2015).

Nonmycorrhizal plant species invasion may reduce the abundance of AM fungi thus negatively influencing the alien plant species that depend on AM fungi. Hence, it further promotes invasion and dominance of non-mycorrhizal plant and hinders the native plant species growth (Vogelsang et al., 2004). One of the nonmycorrhizal invasive plants, *A. petiolata* decreased the proliferation of the native AM fungi and ectomycorrhizal fungi (EMF) (Wolfe et al., 2008). *A. petiolata* reduced the diversity and abundance of AMF due to the production of allelochemicals (Roberts & Anderson, 2001). Another nonmycorrhizal exotic invasive plant species *Tamarix* retarded the growth of native plant *Populus fremontii* S. Watson by interrupting its mutualistic association with AM fungi and EMF (Meinhardt & Gehring, 2012). An invasive plant, *Impatiens glandulifera* Royle in a mixed deciduous forest had a negative effect on the mutualistic association between AM fungi and the native plant *Acer pseudoplatanus* L. (Ruckli et al., 2014). The invasion of another nonmycorrhizal plant, *Reynoutria japonica* Houtt. decreased the species richness and AM fungal abundance due to reduction of organic carbon inputs (Zubek et al., 2016). AM fungi enhance the extensive spread and invasiveness of *Solidago canadensis* more than the native *Stipa bungeana* Trinius plant species (Sun & He, 2010). This clearly shows that AM fungal species facilitates the growth of nonnative species (Yang et al., 2014). Similarly, the invasiveness of *Ambrosia artemisiifolia* L. has been reported due to the positive feedback effect of AM fungi on growth, development, and spread of the species (Fumanal et al., 2006). One of the most aggressive weed, *A. adenophora* increased the AM fungal abundance in highly invaded areas than the non-invaded regions (Niu et al., 2007a). *Pinus* and *Eucalyptus* species were able to invade in the Southern hemisphere only after the introduction of specific EMF (Richardson et al., 1994; Vellinga et al., 2009). *Eucalyptus* has become invasive in Spain following the introduction of the Australian EMF species *Pisolithus* (Diez, 2005).

5. Role of bacterial symbiosis in plant invasion

Although the association between plant root and nitrogen fixing bacteria is one of the most studied symbiotic associations, its importance in plant invasion is largely ignored (Richardson et al., 2000). Invasive plants may form the mutualistic association with nitrogen fixing bacteria *Rhizobium* and actinomycetes *Frankia* (Clawson et al., 1997; Ehrenfeld, 2003). Symbiotic association with *Frankia* promoted successful invasion of *Myrica faya* Ait., in Hawaii (Vitousek et al., 1987). Non-native grass, *Bromus diandrus* Roth grown in lupine soil (*Lupinus arboreus* Sims) accumulated more shoot and root biomass when compared to *B. diandrus* grown in lupine soil. This proved that native lupines promote invasion of invasive grasses and forbs through nutrient enrichment brought about by symbiotic nitrogen fixation (Maron & Connors, 1996). High diversity of nitrogen fixing bacteria (*Arthrobacter*, *Mitsuaria*, *Burkholderia*, *Sinorhizobium*, *Pseudomonas*, and *Rhizobium*) was observed in the rhizosphere of *Ageratina adenophora* invaded areas than in the uninvaded areas (Zhang et al., 2012).

A root nodulating legume, *Cystisus scoparius* (L.) Link seedlings were experimentally grown in old habitat field with or without *Bradyrhizobium* strains inoculum from other existing *C. scoparius* plant in the invasive region and resulted in low biomass and nodulation in absence of inoculum (Parker et al., 2006). A comparison of the genetic diversity of *Bradyrhizobium* associated with *Acacia longifolia* (Andr.) Willd. (invasive leguminous tree) in invaded regions showed that the diversity of *Bradyrhizobium* kept changing since the invasion and higher genetic diversity of *A. longifolia* associated rhizobia were observed in established areas than areas under invasion (Parker et al., 2002). An investigation on the diversity and identity of the rhizobial population nodulating an invasive legume tree *A. mearnsii* in natural *Quercus suber* L., forest revealed adaptation of *Bradyrhizobium* population to new soil environment following invasion (Boudiaf et al., 2014).

Based on the negative effects of invasive plants on the mycorrhizal association, Inderjit and van der Putten (2010) suggested that they may exert similar negative effects on the association between plant symbionts and nitrogen fixing bacteria. The invasion of *Amaranthus viridis* L., restricts the nodulation of *Acacia* sp. and reduces the growth of 30 strains of rhizobia originating from different regions in Africa (Sanon et al., 2011). The nitrogen fixing bacterial endophytes, *Herbaspirillum seropedicae* (Leifson) Ding and Yokota, *Pseudomonas jessenii* Verhille et al., *Sphingobium amiense* Ushiba et al., *Caulobacter vibroides* Henrici & Johnson isolated from invasive grass *Sorghum halepense* (L.) Pers., account for changes in the biochemical cycles (nitrogen, phosphorous and iron) and thus enhance the growth and competitive ability of invasive plants (Rout & Chrzanowski, 2009; Rout et al., 2013).

6. Influence of soil enzymes and nutrients on plant invasion

Exotic alien plant species affect the diversity of soil microbial communities. Soil microorganisms produce soil enzymes that may influence the litter decomposition, soil nutrients availability and ecosystem processes (Aon & Colaneri, 2001; Marchante et al., 2008; Flory & Clay, 2010). Soil pH plays an important role in bacterial and fungal growth and soil enzyme activity (Aon & Colaneri, 2001). Generally, in most of the cases, soil enzymes are considered as the representative of nutrient cycles especially, carbon, nitrogen and phosphorus (Aon & Colaneri, 2001). For example, protease is mostly found in active soil rich in humus and water contents and plays a vital role in mineralization of nitrogen (Utobo & Tewari, 2015), β-glucosidases helps in degradation of plant residues, soil organic matters and has an important function in the carbon cycle. They also increase the soil microbial biomass and hence provide available nutrients for plants (Stott et al., 2010). Phosphatases and ureases are involved in phosphorous and nitrogen mineralization respectively (Sardans et al., 2008). Extracellular enzyme signifies the relationship between microbial activity, litter decomposition and nutrient accessibility (Aragón et al., 2014). Extracellular enzymes break down complex macromolecules into soluble sugars that are used as a source of energy and nutrients by enzyme producing organisms (Burns et al., 2013) They are also known to mineralize nitrogen and carbon (Allison et al., 2006). The resource allocation and growth pattern of native plant species differ from the exotic invasive plants (Liao et al., 2007). Native plants often accumulate greater concentration of specific nutrients that might influence the soil microbial structure and function (Batten et al., 2006). Contrarily, invasive plant species induce changes in the uptake of soil resources especially water and nutrients thus affecting the soil enzyme activity by altering the availability of soil nutrients (Allison & Vitousek, 2004). The response of soil microbial community depends on the metabolites secreted by invasive plant species and result in altered metabolic activity of soil microbes (Marchante et al., 2008). In a greenhouse experiment, endocellulase, aminopeptidase, alkaline phosphatase, and phenol oxidase activities were increased in plant invaded soil when compared with native soil (Kourtev et al., 2003).

Soil enzyme activity depends on the characters of microbial communities and organic matter content in the soil (Allison & Vitousek, 2004). A number of studies were carried out to check the impact of alien plant species invasion on soil enzyme activity (Li et al., 2006; Allison et al., 2006; Fan et al., 2010). Soil under plant invasion [*B. thunbergii* and *Microstegium vimineum* (Trin.) A. Camus] had increased level of chitobiase and aminopeptidase activities that are associated with nitrification while in soil from native plant species (*Vaccinium* sp.) had higher cellulolytic and phosphatase activities (Kourtev et al., 2002). Alkaline and acid phosphatase activities were higher in the areas of *Solidago gigantea* Ait., invasion (Chapuis-Lardy et al., 2006). Similarly, phosphatase and urease activities increased following the *Falcataria moluccana* (Miq.) Barne & J.W. Grimes invasion (Allison et al., 2006). Chacon et al. (2009) observed that both, native and nonnative plant species had almost similar phosphatase activity although the concentration of phosphorous was higher in the roots of the invasive plant, *Kalanchoe daigremontiana* (Raym.-Hamet & H. Perrier) A. Berger. The soil enzymatic activity of acid and alkaline phosphatases as well as the microbial activities of fluorescein diacetate and dehydrogenase was reduced in pasture ecosystem after the introduction of the exotic *Eucalyptus grandis* W. Hill (Liao et al., 2007). The urease activity was higher in *K. daigremontiana* invaded soil than soils under native vegetation (Chacon et al., 2009). Most of the studies indicate that exotic invasive plant species alter nutrient cycling through their influence of soil microbes (Weidenhamer & Callaway, 2010). Plant invasion increased nutrient pool sizes (carbon and nitrogen) and decomposition rates of belowground and aboveground in its invaded regions than native range (Liao et al., 2007). *Lantana camara* L., invasion in India resulted in increased soil nitrogen availability, higher ammonification and nitrification rates (Sharma & Raghubanshi, 2009). Likewise, *Alliaria petiolata* invading soils in the North American temperate deciduous forest were characterized by the higher availability of nitrogen, phosphorous, calcium and magnesium and higher soil pH. Invasion of *C. maculosa* decreased the availability of phosphorous in the soil, but the availability of phosphorous in the soil increased when this weed was eliminated using herbicides (Weidenhamer & Callaway, 2010).

Higher litter inputs of *Eucalyptus camaldulensis* Dehnh. was reported in the riparian soil of invaded region than in the native region (Tererai et al., 2015). Increased concentrations of nitrogen, carbon and phosphorous were recorded in the top 15 cm soil after *Amaranthus viridis* L., invasion (Sanon et al., 2009). Higher growth rates and maximum photosynthetic rates in five groups of invasive species in rainforests of Hawaii than four groups of native plant species were reported (Pattison et al., 1998). The invasive trees, *Ailanthus altissima* (Mill.) Swingle and *R. pseudoacacia* produced more litter than the native trees, thus indicating that invasive species can alter soil properties and litter dynamics (Medina-Villar et al., 2015). *A. longifolia*, a nitrogen fixing invasive tree accumulated litter inputs, thereby increasing the soil nitrogen content and hastened litter decomposition in invaded than in native ranges. Further *A. longifolia* invasion over a longer duration altered the soil properties by increasing the microbial biomass and basal respiration (Marchante et al., 2008). Populations of soil fungi and bacteria mostly correlate negatively with nitrogen mineralization rates leading to altered soil microbial communities which subsequently affect soil nitrogen cycle (Smithwick et al., 2012).

7. Future perspectives and conclusion

Studies on the role of soil rhizosphere microbiota in either promoting or inhibiting plant invasion are increasing. Most of the researchers have shown a microbial shift of the invasive plant species from its native region to its exotic region, but the stage-wise changes occurring during the process of plant invasion is not well known. While a number of studies have focused on soil pathogens and symbionts, the influence of saprophytes and decomposers on plant invasion is largely unexplored. Isolation of microbes from both invaded and uninvaded ecosystems of invasive plant species through modern techniques like, pyrosequencing could provide intense knowledge on identification, abundance, and composition of the soil biota. Additionally, the beneficial and detrimental aspects of isolated microbes in relation to native plant species could also be analyzed. Specific or a particular microbe that colonizes well with the invasive plant in its introduced range could be determined to get a clear idea about plant-soil-microbial interactions. Investigations on soil enzymes and nutrients in both introduced and native habitats for individual native plant species could be useful. The results obtained from the experiments carried out in laboratories or in greenhouse conditions differed from those observed under natural field conditions. Therefore, intensive field studies could provide further knowledge on pre and post changes occurred in both native and exotic ranges.

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