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Soil microorganism impact on the native plant growth under single and co-invasion with invasive plants: Responses through plant-soil feedback

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Abstract

Plant invasion is a key element defining the community structure and dynamics and has become a major concern for the invasive plants to control the restoration of ecosystem diversity. In the same line of thought, soil microorganisms are also considered as a significant parameter of evolution and invasive plants' success. The variations usually overserved in the composition and structure of the soil microorganisms and the consequences of plant invasion. Therefore, understanding the concept of plant invasion and soil microorganism impact plant competition and plant-soil feedback would be a very important step forward in invasive plant control and ecosystem restoration. This review aims to provide a conceptual explanation of plant invasion, the role of soil microorganisms on plant growth and its effects on the native plant-soil feedback and also to demonstrate the importance of understanding the integrative soil microorganism impact on the competition between native and invasive plants along with its effects on plant-soil feedback.

Introduction

A specie is called "invasive'' when it has established itself in a new geographical area and becomes a disturbance and notice agent for biodiversity. The term biodiversity refers to the range of existence of one or many organisms with specific diversity or floristic diversity to discuss the diversification of plant species and addresses intraspecific variability, as well as functional diversity to define a group of species [1, 2]. Numerous studies have shown large declines in biodiversity areas that are heavily invaded by exotic plants leading some researchers in one hand to conclude that such invasive species are one of the most important threats to biodiversity across the planet [3-5] and on the other hand plant invasions are rarely implicated as the cause of species extinctions such as termination of an organism or group of an organism called taxon and usually species either regionally or globally [6-8]. However, the effects of introduced plant species on patterns of biodiversity still need more clarification [6]. It has been suggested that the majority of the native plant extinction caused by invasive plants is the result of an association of living organisms including micro-organisms interacting together for their nutrition [9-11] rather than competition within trophic levels while invasive plants are rather innocuous [6, 12]. These disparate points of view, along with a variety of other piecemeal evidences have penetrated into the public table and have incited many scientists to investigate whether the invasive species are really harmful to the native plants. The competition is a relationship between organisms in which one is harmed when both are using the same resources for their growth, reproduction, or survivability [13, 14]. It can occur between plants of the same family, or between plants from different families. The invasive plants are generally considered superior to native plants in terms of competitiveness. Moreover, it has been suggested that the species with similar niches and/or in closely related species present the strongest competition capacity [14]. However, the outcome of this antagonism is strongly context-dependent as competitive strength varies along with environmental conditions, life stages, as well as soil microorganisms [15]. Non-native species have to overcome numerous barriers to naturalize and become invasive in the introduced range [14]. The soil contains a variety of microorganisms and organic compounds that can be toxic or non-toxic for the seeds and roots [16]. The concept of competition for nutrients constitutes the most direct interactions between plants and soil microorganisms [11, 17]. Indeed, strong positive and negative relationships exist at the extra and intraspecific levels through mechanisms of facilitation, symbiosis, and parasitism [18]. Therefore, understanding the competition from exotic plants and soil microorganisms impacts individually and interactively affect native plant performance would be a great achievement which can be useful for invasive plant management and control and ecosystem restoration. Nevertheless, the impact of the invasive plant on native plant such as the soil microorganism effects in invasive plant invasiveness and native plant extinction deserves more consideration. Additionally, the plant-soil feedback defined as a process where plants alter the biotic and abiotic qualities of the soil grow in, alters the ability of plants to grow in the same soil in the future [19, 20], it can include changes in chemical compounds such as carbon storage, soil salinity and soil chemistry.

A large number of mechanisms have been proposed to explain the invasive plants' success including plant-soil feedback which has been widely proposed and tested over the past two decades [21], as an important concept explaining the invasive plant invasiveness and soil microbial composition effects on the functioning of the ecosystem. Plant-soil feedback plays an important role in plant-plant and plant-soil interaction and has been widely recognized as the plant-influenced changes to the soil microbial community that then positively or negatively affects subsequent plant growth [22]. Various studies on plant-soil feedback approached soils as a black box, which can be modified by plants and soil microorganism interactions [23]. The invasive plants can modify soils in a way that benefits their fitness more than the native plants [13]. However, it is unclear how competition among plant species alters the strength and direction of the plant-soil feedbacks. Therefore, the effects of soil microorganism on invasive plants invasiveness and its impact on plant-soil feedback need further studies [24]. The main aims of this work includes a conceptual explanation based on literature review and understanding of the concept of plant invasion and plant-soil feedback, to discuss the role of the microbial community on the co-invasion and its effects on the native plant-soil feedback and to demonstrate the importance of understanding the integrative soil microorganism impact on the competition between co-invasive and native plants and its effects on the plant-soil feedback.

Soil Biota and Plants Interactions

The mutual or reciprocal action or influence between plant and soil biota that refers to the interaction between soil biota and plants has been the focus of many studies [25-27]. The soil biota can be influenced by invasive plants via direct and indirect mechanisms [28]. Many researchers have been investigating plant-soil interactions which can be considered as the cause of the evolutionary changes in invasive plants and understanding the mechanisms underlying these interactions is indispensable to elucidate the role of environmental conditions and plant traits differences in the successful establishment of the invasive plants [29]. A better understanding of post-invasion changes could be provided by the assessment of shifts in the microbial communities and their subsequent influence on native and invasive plants competition [30]. Many studies on plant-soil interactions suggest that the introduction of exotic plant species has the potential to alter the microbial structure, function and chemical components of the soil [31]. For instance, Kourtev et al. [32] in 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 variations in the structure and function of microbial communities in all the three species [32]. The interaction between microorganisms and plants can vary from mutualism (association between organisms of two different species in which each benefit) to parasitism [33]. The invasive plant-soil microbial interactions differ from their native and non-native ranges [34]. For example, the soil microbial communities of many invasive plants in their native milieu differ from the invaded regions [35], which explain the differences observed in plant growth and survival capacity in different zones. Plants modify soil microbes in a way that results in negative plant-soil feedback which occurs when plants are less able to grow in soil that was previously occupied by a member of the same species, or positive plant-soil feedback. Positive plant-soil feedback occurs when plants are able to grow in soil that was previously occupied by the same species [36]. Kuebbing & Nuñez, in 2014 stated that among the important number of invasive plant interactions which have been investigated, 39.8% showed negative plant-soil feedback and only 18.9% exhibited positive plant-soil feedback [37] interactions and this statement has been supported by Callaway in 2010 who demonstrated that invasive plant species interrupts both the long-term coevolved interactions among the native plants, and the native plant-microorganism association [38]. For instance, changes in the composition of AM fungi were observed over two growing seasons in S. canadensis invaded regions [39]. These feedback processes may, in turn, affect the ecological processes, species interactions and temporal dynamics of plant communities.

Plants selectivity influence rhizosphere microbiota and establish feedback interactions [40]. Among all the soil biota, most of the terrestrial plants form a symbiotic association with the soil mycorrhizal fungi [23]. Though mycorrhizal associations are usually presumed to be mutualistic, the nature of the association can change from mutualism to parasitism depending upon the plant species and environmental conditions [41]. Invasive plants generally promote favorable soil microbes by establishing positive feedback [42] and suppress harmful microorganisms by developing some mechanism that enhances the growth of beneficial microorganisms such as AM fungi [43]. For instance, Yang et al. in 2014 demonstrated that invasive plant; *Solidago canadensis L*. affects the composition of mycorrhizal fungi by promoting the beneficial Arbuscular Mycorrhizal fungi and suppressing the detrimental microorganisms harmful to its growth.

Soil Microorganism Impact

Soil Microorganism Effect on the Growth of the Native Plant under Invasion

While most invasive plants persist only through small isolated populations during the invasion process, others have harmful biological invasion behavior. There are large populations that disperse through landscapes and may compete with native plants and alter the functioning of ecosystems. The consequences and impacts of invasive plants on the native plant growth differ depending on the native itself the invasive plant identity, the soil microorganisms and the type of invasion. How the mechanisms underlying the soil microorganism's impact on soil properties which have been the focus of many researchers during the last two decades still need further studies.

The soil microorganisms can affect plant productivity favorably or unfavorably, either indirectly by modifying physical or chemical properties, or directly through interactions with plant roots [38]. The soil microorganisms can have

profound effects on ecosystem invasion and the competition between that invasive and native plant. The variety of plant-soil interactions might be the factor enhancing invasive plant invasiveness in the invaded range [34] and this statement is in line with many studies that confirm that the soil microorganism's impact on plant growth depends on the type of the soil and its origin. The Plant evolution and growth parameters are significantly better in soils irrigated with the native plant litter as compared to soils watered with the invasive plant litter. Moreover, it is well known that litter input impacts the soil microorganism composition, and its decomposition affects clearly plant growth. For instance, on one hand, the soil microorganisms do not have much impact on the invasive *Acacia dealbata* establishment, suggesting that the hypothetical changes that the invasive Acacia litter have on soil microbial community from native range might not affect its own growth. On the other hand, continuing invasion by *A. dealbata* can adjust soil properties beneficial for its growth [44].

Altogether, prove that the invasive *A. dealbata* growth is undoubtedly favored in soils previously impacted by the same plant, due to the significant augmentation of the nutrient content observed in soil and the creation of compatible operative nitrogen-fixing microorganisms [45]. Numerous studies suggested that soil microorganisms play an essential role in the completion between an invasive plant and native plant as well as invasive plant invasiveness by decomposing organic matter, cycling nutrients, and fertilizing the soil which directly affects plant growth and plant invasiveness [46].

Impact of soil microbial communities on native and invasive plant competition

Plant traits vary at the same time with the soil properties and composition such as soil fertility and soil microbial communities, but to prove whether it's due to the environmental conditions or plant-soil feedback is not yet straightforward, especially in long-lived plant communities. It is difficult to state with confidence that co-variation between soil microbial community and exotic plant traits is the outcome of environmental conditions without investigating specifically the potentiality of soil microbial community to influence the invasive plant's properties. Since each ecosystem is characterized by its own soil microbial community, its impact on plant growth will depend on the plant itself and the ecosystem in which it grows. It has been suggested invasive plants have the capability to cope with the soil microbia which is an advantage over the native plants. For instance, the interactions between nonmycorrhizal fungal endophytes and the AM fungi are known to enhance plant invasiveness [47]. This AM fungi secrete hormones that are usually beneficial to the invasive plants and increase their competitive ability as compared to the native plants [48].

Many hypotheses including the enemy release hypothesis, mutualism hypothesis, enhanced mutualism hypothesis, degraded mutualism hypothesis; accumulation of local pathogen hypothesis, and novel weapon hypothesis which shown clearly the relationship between the soil microbes and plant invasion. One of the most pronounced mechanisms is the enemy release hypothesis which states that the absence of antagonists during colonization resulting in the successful establishment of invaded plant species [49]. For instance, *Hypericum perforatum L*., which is a native plant in Europe, the western part of Asia and the northern part of Africa, experienced reduced herbivores in its exotic range than in its native range. Similarly, in *Ammophila Arenaria (L.)* link invaded regions, the pathogenic nematodes were less abundant than their native regions. 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 [50] suggests that invasive alien plant species gather native soil pathogen that restricts native plant spread and growth [51]. 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 or inhibit their growth faculties. Also, the novel weapon hypothesis state that invasive plants possess new biological weapons that function as strong allelopathic agents for new plant-soil-microbial interactions [52] and plant-soil feedback systems [53]. A case study on *Alliaria petiolata* conducted by *M. Bieb Cavara* & Grandetate found that *Alliaria petiolata* 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 biochemical [54]. In contrast, *A. petiolata* in its native range failed to exhibit any inhibitory effect on mycorrhizal fungi [54].

In addition, according to the enhanced mutualism hypothesis, many invasive plant species have a better association with soil mutualists in its introduced ranges than its native ranges that lead to successful invasion [43]. The degraded mutualism hypothesis suggests that invasion of an area by non-mycorrhizal plant reduces the abundance of arbuscular mycorrhizal (AM) fungi. Conclusively, it's been suggested that both plants and microorganisms obtain their nutrients from the soil and change soil properties through organic litter deposition and metabolic activities, respectively. Microorganisms have a range of direct effects on plants since their communication with the microorganisms is through metabolites exuded by the roots. The figure below gives more details about the major knowledge gaps for understanding the mechanisms of plant-microbe interactions in the rhizosphere are shown in bold (**Fig. 1**).

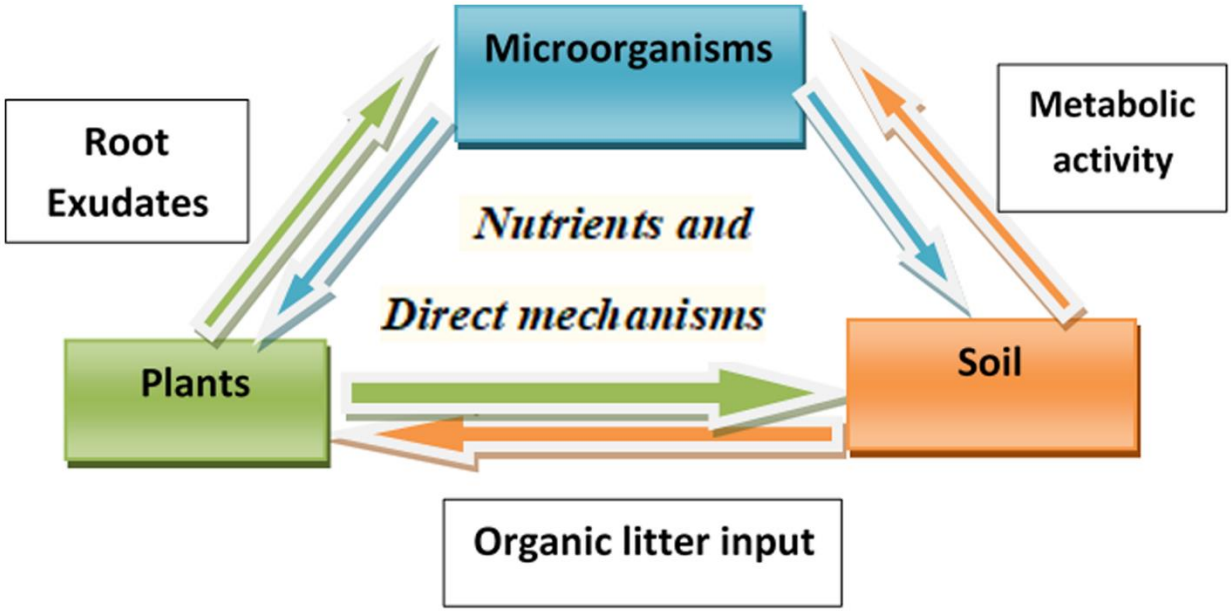

Fig. 1: Interactions between plants, microorganisms, and soil

Impact of soil microbial communities on the invasive plant invasiveness

Many plants are introduced into a new environment either naturally or deliberately where they proliferate and establish successfully. It has been confirmed that more 13,000 plant species are growing outside their native range [55]. A species becomes locally dominant when introduced into a small area proliferates rapidly and transforms the multispecies communities into mono-dominants. The plant species that alter the natural plant communities are commonly termed an invasive plant species [56]. Nevertheless, the factors determining plant invasion and invasive plant success are still not well understood [57]. Generally, the biological invasion is of major concern as it causes global environmental changes; alter the structure and function of ecosystems, biodiversity loss of biodiversity as well as native plant extinction. In the same way, the biogeochemical cycling of nutrients which can be influenced by the identity of the plant community might be altered due to plant invasion [31]. However, invasion plant establishment and expansion also depend directly or indirectly on anthropogenic factors that confirm an indispensable plant-soil and soil microorganisms' interactions.

These interactions play a great role in the successful establishment of invasive plant species. Soil microorganisms are also involved in several important processes for invasive plant success and establishment. For instance, mycorrhizal fungi and bacteria affect the diversity and abundance of belowground soil organisms and therefore can be substantial in response to plant invasion [58]. The compositions of soil microbial communities of invasive plants are different and have altered ecosystem functions from those of native plant

species. It has been suggested that soil microbes are one of the key components that either facilitate or inhibit plant invasion [24, 43, 59]. Therefore, elucidating the interactions between soil microbes and exotic invasive plant species provide a better understanding of the ecological roles of the soil biota in invasive plant success. It has been previously suggested that plant invasion could alter the physical and chemical properties of the soil [60-62]. For instance, the invasion by *Acacia saligna* increases soil moisture and temperature [63]. In addition, soil pH in one hand can be increased by plant invasion [64], and on the other hand, plant invasion may decrease soil pH.

Soil Biota and Plant-soil Feedback System

Plants can modify the structure and chemical characteristics of the soil which in turn influence their performances. This process is commonly termed as plant-soil feedbacks (PSF) [65]. The PSF is a well-known invasion mechanism that operates in a natural system and can be either positive or negative. The positive feedback is mostly favored by mycorrhizal fungi, nitrogen-fixing bacteria, and beneficial soil microbes [66], and negative feedback is mediated by soil-borne pathogens, herbivores, and parasites [67]. Soil biota exercises different impacts on native and invasive ranges [34]. Positive feedback promotes intraspecific competition and predominance of plants due to the presence of symbiotic mutualists that enhance plant growth thus increases interspecific competition [68]. However, the negative feedback regulates and maintains not only the plant abundance but also the coexistence of other plant species [67, 69]. For instance, the soil biota associating with Centaurea maculosa Lam., presents negative effects on the plant under native European soils in the absence of competitors. However, 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 the exotic plants through positive feedback effect [70]. Moreover investigations on plant-soil biota feedback of 10 congeneric pairs of native and non-native herbaceous plant species showed more significant negative native plant-soil feedback as compared to the invasive plants [71]. Nevertheless, invasive plant species causes significant changes in soil conditions in their new range by producing organic or inorganic compounds that suppress the soil biota. For instance plant-soil interaction of the invasive *Triadica sebifera (L.)* presents negative effects in its native range and positive effect on invaded soil range [26]. It has been suggested that native plants experience more often negative plant-soil feedback as compared to invasive plants.

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Conflict of interest

The authors declare no conflict of interest.

Conclusion

The plant invasions are widely recognized as the main distress and constitute the cause of ecosystem deterioration and native plant extinction. The invasive plant management and control and invasive plant invasiveness, the actual and precise mechanism underlying the invasive plant success is still not well understood. The changes observed in the physical and chemical properties in the soil are due to the plant invasion and the soil microorganisms which is considered as an important connection between the plant and soil but also determining the plant growth and its establishment. The serious field experiments might bring significant understanding and clarification in the modification resulting from plant invasion in native and invasive ranges. A better understanding of the concept of the plant invasion and soil microorganism impact in plant-soil feedback would be a significant step forward in invasion plant control and ecosystem restoration.

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