

Research Article

Shortcomings of Present Studies on the Effects of Invasive Plants on Soil Microbial Communities

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Abstract

One of the principal reasons for the successful invasion of invasive plants is that these invaders can facilitate the succession of soil microbial communities in their rhizosphere. This study presents a summary of the effects of invasive plants on soil microbial communities. The effects of invasive plants on soil microbial communities encompass both indirect and direct effects. These include changes in the physicochemical properties (e.g., pH, moisture, and electrical conductivity); alterations in enzyme activities related to nutrient (especially nitrogen) cycling, and nutrient (especially nitrogen) availability levels in soil; variations in the growth performance of invasive and native plants, and the species composition of native plant communities; and changes in the alpha diversity, the relative abundance, the metabolic activity, and the community structure of soil microorganisms (especially the dominant microbial species). In general, invasive plants can cause changes in the structure of soil microbial communities (particularly functional microorganisms, such as the mycorrhizal fungi and N-fixing bacteria) in invaded ecosystems in ways that provide positive feedback for their invasiveness and negative feedback for the growth performance of native plants. This review also considers the limitations of existing studies on the effects of invasive plants on soil microbial communities. The results will provide a solid theoretical basis for elucidating the role of the interactive feedback between invasive plants and soil microbial communities in driving the successful invasion of invasive plants.

Introduction

One of the primary reasons for the successful invasion of invasive plants is that these invaders can facilitate the succession of soil microbial communities in their rhizosphere, thereby strengthening the microbial functions to accelerate their further invasion process, i.e., invasive plants can create interactive feedback with soil microbial communities during their invasion process [1,2].

In light of the aforementioned findings, a review of the effects of invasive plants on soil microbial communities was conducted, along with an examination of potential avenues for future research in this field.

Effects of invasive plants on soil microbial communities

In general, invasive plants can affect soil microbial communities primarily through two main processes: litter decomposition and/or the secretion of root exudates (Figure 1). The effects of invasive plants on soil microbial communities encompass both indirect and direct effects, mainly including changes in the physicochemical properties (e.g., pH, moisture, and electrical conductivity); alterations in enzyme activities related to nutrient (especially nitrogen) cycling, and nutrient (especially nitrogen) availability levels in soil; variations in the growth performance of invasive and native plants, and the species composition of native plant

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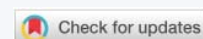
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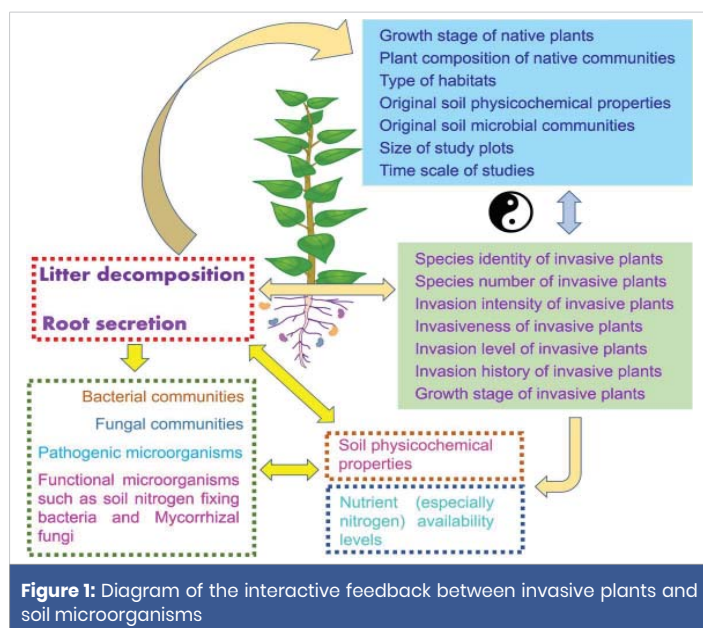
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communities; and changes in the alpha diversity, the relative abundance, the metabolic activity, and the community structure of soil microorganisms (especially the dominant microbial species) (Figure 1).

However, a considerable number of studies have demonstrated that the effects of invasive plants on soil microbial communities are inconsistent, exhibiting a range of effects, including positive, negative, and neutral effects [3,4]. These inconsistent results may be attributed to several factors, including differences in the species identity, the species number, the invasion intensity, the invasiveness, the invasion level, and the invasion history of invasive plants, the growth stage of invasive and native plants, the plant composition of the studied communities, the type of habitats, as well as the original physicochemical properties, and the original microbial communities in soil, the size of the study plots, and/or the time scale of the studies.

In general, invasive plants can alter soil microbial communities (particularly functional microorganisms, such as the mycorrhizal fungi and N-fixing bacteria) in invaded ecosystems in ways that provide positive feedback for their invasiveness and negative feedback for the growth performance of native plants [3,5] (Figure 1). In particular, invasive plants can benefit from the changed interactions with soil communities, especially functional microorganisms (e.g., mycorrhizal fungi, which can improve the plant's disease resistance as well as can also enhance the efficiency of nutrient utilization, etc.), and by disrupting the mutualistic interactions between soil microbial communities and native plants [1,6]. However, invasive plants are facultative soil functional microorganisms (e.g., mycorrhizal fungi), which either have weak or no dependence on the microscopic symbionts, depending on the environment. This may result in invasive plants gaining a stronger competitive advantage

through degenerating the mycorrhizal symbiont networks on which several native plants depend [6] or receive great benefits from the associations with the microscopic symbionts, which may result in invasive plants reducing their dependence on the microscopic symbionts [7] and/or changes to the community of the microscopic symbionts [6] and/or variations to the community of the microscopic symbionts [8]. This alternative dependence may be a successful strategy for numerous invasive plants. As an important element in the survival and competition of native plants, the absence of mycorrhizal symbiosis could alter the competitive outcome of these dominant native plants [9,10].

Shortcomings of present studies on the effects of invasive plants on soil microbial communities

Several studies have recently examined the effects of invasive plants on soil microbial communities. However, the current study still has some shortcomings that need to be analyzed in more depth in the follow-up work, such as:

(1) Existing studies have mainly focused on the effects of invasive plants on soil bacterial and fungal communities, with less attention devoted to the effects on soil functional microbial communities, except mycorrhizal fungi.

(2) How can the contribution of soil microbial communities (including one microbial species/taxa (e.g., N-fixing bacteria) and all microbial species/taxa (including soil bacterial and fungal communities, soil functional microbial communities, and soil pathogenic microorganisms)) to the invasiveness of invasive plants be quantitatively assessed? To what extent do soil microbial communities play a role in the invasion process of invasive plants? What are these key mechanisms that underpin this process?

(3) Which microbial species/taxa contribute most to the invasiveness of invasive plants? Do microbial species/taxa with the highest relative abundance contribute most to the invasiveness of invasive plants? Do significantly altered microbial species/taxa under the invasion process of invasive plants contribute most to the invasiveness of invasive plants? Which factors are critical in facilitating or limiting the contribution of soil microbial communities to the invasiveness of invasive plants? Is there a habitat dependence, nutrient level dependence, nutrient type dependence, disturbance intensity dependence, disturbance type dependence, disturbance history dependence, invasive plants' species identity dependence, invasive plants' species number dependence, invasive plants' invasion history dependence, and invasive plants' invasion level dependence in the species composition of microbial species/taxa that contribute most to the invasiveness of different invasive plants? What are these key mechanisms?

(4) How do microbial taxa such as soil bacterial and fungal communities, soil functional microbial communities, and soil

pathogenic microorganisms interact with each other during the invasion process of invasive plants? How is the strength of these interactions measured? How do they contribute to the invasiveness of invasive plants? Is there an additive, antagonistic, or neutral effect of soil bacterial and fungal communities, soil functional microbial communities, and soil pathogenic microorganisms on the invasiveness of invasive plants? What are these key mechanisms?

(5) How do microbial taxa such as inter-root/epidermal flora and endophytic flora interact with each other during the invasion process of invasive plants? How is the strength of these interactions measured? How do they contribute to the invasiveness of invasive plants? Is there an additive, antagonistic, or neutral effect of inter-root/epidermal flora and endophytic flora on the invasiveness of invasive plants? What are these key mechanisms?

(6) The main direct pathways by which invasive plants affect soil microbial communities are through the process of litter decomposition and/or the secretion of root exudates. Are the effects of above-ground and below-ground interactions synergistic, antagonistic, neutralizing, or other mechanisms? What are these key mechanisms?

(7) Invasive plants can indirectly affect soil microbial communities by affecting soil physicochemical properties and nutrient availability levels, etc. So, how can the direct and indirect effects of invasive plants on soil microbial communities be measured? Conversely, how can direct and indirect changes in the soil microbial communities under the invasion process of invasive plants contribute to the invasiveness of invasive plants? What are these key mechanisms?

(8) The invasion process of one invasive plant consists of various levels of invasion processes, including light, moderate, and heavy invasion [11,12]. Is the contribution of one microbial species/taxa (e.g., N-fixing bacteria or mycorrhizal fungi) to the invasiveness of the same invasive plant at different levels of invasion equivalent? At what level of invasion do soil microbial communities contribute most to the invasiveness of the same invasive plant? What are these key mechanisms?

(9) In addition to the important role of soil microbial communities in the invasion process of invasive plants, some insects (especially the pollinators and predators) and birds (especially those birds that can pollinate and spread the propagules of invasive plants) may play a key role in the successful invasion of numerous invasive plants (especially heterogamous pollinated invasive plants and invasive plants whose seeds are primarily animal-borne) [13,14]. So, how can the contribution of soil microbial communities and these animals to the invasiveness of the same invasive plant be quantitatively assessed?

(10) Even after invasive plants are removed, their effects on the habitats can last for some time, a phenomenon known

as the legacy effects of invasive plants [15,16]. How can the influence of the legacy effects of invasive plants on soil microbial communities be quantitatively assessed? What are the key factors that determine the legacy effects of invasive plants on soil microbial communities? How long do the legacy effects of invasive plants on soil microbial communities last before they are considered to have completely “disappeared”, and what are the criteria for measuring this? Do the legacy effects of invasive plants on soil microbial communities contribute to the successful invasion of themselves and other invasive plants in the future? Is there habitat dependence, nutrient level dependence, nutrient type dependence, disturbance intensity dependence, disturbance type dependence, disturbance history dependence, invasive plants’ species identity dependence, invasive plants’ species number dependence, invasive plants’ invasion history dependence, and invasive plants’ invasion level dependence in the duration of the legacy effects of invasive plants on soil microbial communities? What are these key mechanisms?

(11) The co-invasion of multiple invasive plants often occurs in the same habitat [17,18]. Does the contribution of soil microbial communities to the invasiveness of invasive plants increase as the number of invasive plants increases during the co-invasion process mediated by multiple invasive plants? Is the contribution of one microbial species/taxa (e.g., N-fixing bacteria or mycorrhizal fungi) to the invasiveness of multiple invasive plants co-invading an ecosystem equivalent? Is the contribution of all microbial species/taxa (including soil bacterial and fungal communities, soil functional microbial communities, and soil pathogenic microorganisms) to the invasiveness of the same invasive plants under the co-invasion equivalent? Which microbial species/taxa are more likely to contribute to the creation of co-invasion? In which habitat do soil microbial communities contribute most to the invasiveness of multiple invasive plants co-invading an ecosystem? How can the effects of the contribution of soil microbial communities on the invasiveness of earlier successful invasive plants on the invasiveness of later successful invasive plants be quantitatively assessed? How can the effects of the contribution of soil microbial communities on the invasiveness of the later successful invasive plants on the invasiveness of the earlier successful invasive plants be quantitatively assessed? Are the effects of the contribution of soil microbial communities (including one microbial species/taxa (e.g., N-fixing bacteria) and all microbial species/taxa (including soil bacterial and fungal communities, soil functional microbial communities, and soil pathogenic microorganisms)) on the invasiveness of multiple invasive plants co-invading an ecosystem through synergistic, antagonistic, neutralizing, or other mechanisms? What are these key mechanisms?

(12) The invasion resistance of native plant communities plays a key role in preventing the invasion process of invasive plants [18,19]. What role do soil microbial communities

(especially soil functional microbial communities and soil pathogenic microorganisms) play in the invasion resistance of native plant communities to the invasion process of invasive plants? Do native soil microorganisms and invasive microorganisms play the opposite role in the invasion resistance of native plant communities? Do these native soil microorganisms actively resist the invasion process of invasive plants and actively become the “national heroes” of native soil microorganisms, or do they actively league with invasive plants to facilitate the invasion process of invasive plants, and be motivated to become the “traitors” of native soil microorganisms? Are the effects of invasive microorganisms on the invasiveness of invasive plants positive, but pose negative effects on the growth performance of native plants? What are these key mechanisms?

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