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Do forest soil microbes have the potential to resist plant invasion? A case study in Dinghushan Biosphere Reserve (South China)

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ABSTRACT

Successful invaders must overcome biotic resistance, which is defined as the reduction in invasion success caused by the resident community. Soil microbes are an important source of community resistance to plant invasions, and understanding their role in this process requires urgent investigation. Therefore, three forest communities along successional stages and four exotic invasive plant species were selected to test the role of soil microbes of three forest communities in resisting the exotic invasive plant. Our results showed that soil microbes from a monsoon evergreen broadleaf forest (MEBF) (late-successional stage) had the greatest resistance to the invasive plants. Only the invasive species *Ipomoea triloba* was not sensitive to the three successional forest soils. Mycorrhizal fungi in early successional forest *Pinus massonina* forest (PMF) or mid-successional forest pine-broadleaf mixed forest (PBMF) soil promoted the growth of *Mikania micrantha* and *Eupatorium catarium*, but mycorrhizal fungi in MEBF soil had no significant effects on their growth. Pathogens plus other non-mycorrhizal microbes in MEBF soil inhibited the growth of *M. micrantha* and *E. catarium* significantly, and only inhibited root growth of *E. catarium* when compared with those with mycorrhizal fungi addition. The study suggest that soil mycorrhizal fungi of early-mid-successional forests benefit invasive species *M. micrantha* and *E. catarium*, while soil pathogens of late-successional forest may play an important role in resisting *M. micrantha* and *E. catarium*. The benefit and resistance of the soil microbes are dependent on invasive species and related to forest succession. The study gives a possible clue to control invasive plants by regulating soil microbes of forest community to resist plant invasion.

1. Introduction

The resistance of forest community to invasion has been one of the hotspots in ecology (Lonsdale, 1999; Levine et al., 2004; Richardson and Pyšek, 2006; Zhang et al., 2010). It is generally assumed that undisturbed closed-canopy forests, especially late-successional forests, are highly resistant to plant invasions (Holle et al., 2003; Levine et al., 2004; Domènech and Vilà, 2006), while the disturbed and early-successional forests are easy to be invaded by exotic plants (Freestone et al., 2013). Different plant species can influence soil microbial communities (Grayston et al., 1998; Berg and Smalla, 2009; Ladygina and Hedlund, 2010). Plants have different abilities to influence their abundance by changing the structure of their soil communities (e.g. Arbuscular mycorrhizal fungi (AMF) communities, pathogen communities), and that this is an important regulator of plant community structure (Klironomos, 2002). In the process of forest succession, soil biota varies at certain order like light, plant species, biodiversity and community function which are regarded as sources forming community resistance (Fine, 2002; Jia et al., 2005; Martin et al., 2008).

A meta-analysis of the several relevant studies by Levine et al. (2004) pointed out that soil microbes, particularly mycorrhizal mutualists, play a critical role in determining patterns of abundance and invasiveness of certain species. AMF are crucial to the functioning of ecosystems in view of their wide spread mutualistic association with most known plant species (Shah et al., 2009; Smith and Read, 2010). Many studies indicate positive effect of AMF in plant invasions (Marler et al., 1999; Reinhart and Callaway, 2006; Walling and Zabinski, 2006; Shah et al., 2009; Zhang et al., 2010). Non-native plant species have a symbiotic relationship with AMF that would make invasion succeed by increasing the efficiency of

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nutrient absorption and the resistance to drought, heavy-metal toxicity or disease (Augé, 2001; McHugh and Dighton, 2004; Wu et al., 2013). Although most native AMF facilitate invasion of exotic plants, pathogens in local soil restrict exotic plants (Levine et al., 2004), some studies in recent years found that local soil has negative effects on invasive plants which may relate to pathogenic fungi, bacteria and virus (Van der Putten and Peters, 1997; Kulmatiski et al., 2008).

Successful invaders must overcome biotic resistance, the reduction in invasion success caused by the resident community (Levine et al., 2004). Pathogens are important components in community's resistance to exotic plants invasion. Some native plant species increase resistance to invasion by accumulating pathogens that inhibit biomass of exotic plants (Callaway et al., 2013; Gao et al., 2013). Pathogen accumulation on invasive plant species may result from high plant densities, expending geographical ranges, host range shifts and adaptation of native pathogens to invasive species (Flory and Clay, 2013). And some native pathogens have been tried to apply in control of invasive plants (Müller and Nentwig, 2011; Fowler et al., 2012; Van Wilgen et al., 2013). An understanding of biotic resistance might be used to predict which communities are most susceptible to invasions or where invasions are most likely to occur (Levine and D'Antonio, 1999). Similarly, restoration ecologists need to design communities that will best resist invasion (Seabloom et al., 2003; Corbin and D'Antonio, 2004). Thus, it is urgent to understand the effect of soil microbes on community resistance, and to provide a reference for community construction with great resistance to invasive plants. However, we know little about forest community in resisting plant invasion from the point view of soil microbes.

Pinus massonina forest (PMF), pine-broadleaf mixed forest (PBMF) and monsoon evergreen broadleaf forest (MEBF) are three forest types that are located along the gradient of successional sequences in Dinghushan Biosphere Reserve (DBR). PMF, PBMF and MEBF represent early-, middle- and late-succession forests, respectively (Peng and Wang, 1993; Peng et al., 2010). The soil microbial community structures were reported to differ significantly among the PMF, PBMF and MEBF in Dinghushan Biosphere Reserve (Yi et al., 2005; Liu et al., 2012). Furthermore, soils from the three forest communities showed different inhibition capacities for the growth of the invasive plant *Mikania micrantha* (Hou et al., 2011).

Therefore, we selected three successional forest in DBR in southern China. Using the methods of soil sterilization and microbe inoculation, we investigated whether soil microbes along a gradient of successional sequences contributed to resistance to invasive plants. Here, the specific questions we evaluate are: (i) What are the effects of soil microbes of different successional forests on growth of several exotic invasive plants? (ii) what is the role of mycorrhizal fungi and pathogens plus other non-mycorrhizal microbes in resisting exotic invasive plants?

2. Materials and methods

2.1. Study site

The Dinghushan Biosphere Reserve (DBR), which has representative zonal vegetation of lower subtropical forest, is located in Zhaoqing, Guangdong, China (23°10′N, 112°35′E). It has a monsoon climate and is located in a subtropical moist forest life zone. The mean annual temperature is 22.3 °C and the mean annual rainfall is 1678 mm, which has a distinct seasonal pattern. Monthly air temperature and precipitation representing the DBR's climatic regime were obtained from the Gaoyao Weather Station, 10 km from DBR (Zhou et al., 2011). The soils in DBR are mainly lateritic red soil, yellow soil and mountain scrubby-meadow soil developed from sandstone and shale.

2.2. Plant species

We selected three invasive Asteraceae species (*Mikania micrantha*, *Eupatorium catarium*, *Biodens pilosa*) and one invasive Convolvulaceae species *Ipomoea triloba* L. (Table 1).

2.3. Effects of soil microbes on growth of exotic invasive plants (Experiment 1)

We collected soil from three forests PMF, PBMF and MEBF along a successional sequence in DBR. Each forest soil was sampled from five quadrates (10×10 m^2). Twenty subsamples (about 2 kg per subsample) were collected within each quadrate from the top 10-cm soil. Soil samples of each forest soil were mixed and sieved (Φ 2 mm) to remove big root and stones, 2/3 of the soil from each forest was watered and kept fresh, which was further divided into halves for control and fungicide treatment, and the rest 1/3 was triple-autoclaved on three successive days to kill the microbial community (refer to Callaway et al., 2004).

Seeds of the four invasive weeds were all collected from Xiaoguwei Island, Guangzhou, China in November 2013. The seeds were surface sterilized with 1% sodium hypochlorite and then they were seeded in sterilized commercial soil and placed in chamber with 15–20 days cultivation. We transplanted uniform seedlings in pots (12 cm diameter × 11 cm height without holes at the bottom) filled with 1000 g collected original forest soil (non-sterilized origin soil), treated (sterilized, fungicide) forest soil, respectively. Each pot contained one individual. Each species per treatment per soil origin was replicated five times. One week later, we started fungicide (Benomyl) treatment. We applied 100 ml of 0.2 g/L Benomyl solution to the fungicide pots biweekly to maintain the effectiveness of fungicide (Kahiluoto et al., 2000; Cahill et al., 2008). To keep the plants grow well during winter, all plants were placed in growth chambers (PQX-1000 A, Ningbo Instruments, China) with 75% relative humidity and a 12 h/12 h light/dark cycle at 28/25 °C. The conditions of all chambers were monitored and adjusted every day. The plants were watered every two days for 12 weeks until harvested. Pot positions were thoroughly randomized. To maintain uniformity of the growth conditions and to make up for the limitation of chambers and avoid the deviation of the manipulating conditions among the chambers, the pots were switched from one chamber to another every two weeks.

2.4. Role of mycorrhizal fungi and pathogens plus other non-mycorrhizal microbes in resisting exotic invasive plants (Experiment 2)

In exp. 1 we tested the effects of soil microbes in resisting exotic invasive plant growth through sterilizing soil and applying fungicide to soil. To test the role of mycorrhizal fungi and pathogens of the three forests soil (PMF, PBMF and MEBF) in resisting exotic invasive plants, we conducted an inoculation experiment with extracted mycorrhizal fungi, pathogen and other non-mycorrhizal microbes from the original soil of the three successional forests. Mycorrhizal fungi and pathogen plus other non-mycorrhizal microbes were extracted from the original soil of the three successional forests by wet sieving. And then we added the extracted spores into collected sterilized homogeneous soil to test their role in invasive plants.

All subsamples were passed through a 150-μm sieve to eliminate larger organisms. Then we extracted mycorrhizal fungi and soil pathogen communities using a wet-sieving method