



Co-invasive exotic pines and their ectomycorrhizal symbionts show capabilities for wide distance and altitudinal range expansion



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ABSTRACT

We asked if exotic *Pinus elliottii* seedlings can survive and form ectomycorrhizas at higher elevations and long distances from their current range, and which ECM partners disperse to these soils. We selected three plots at four grassland sites along an altitudinal gradient (900, 1600, 2200, and 2700 m asl) established at c. 110, 3000, 6000, and 9000 m from the closest pine plantation, respectively. We combined field experiments with glasshouse assays to assess survival and ECM fungi in roots and soils. A pine plantation close to the lowest site was also selected for DNA metabarcoding of soils. Pine seedlings survived at all altitudes but not all formed mycorrhizas. They formed mycorrhizas with *Suillus granulatus* at 900, 1600, and 2200 m asl (i.e. up to 6000 m from the closest pine plantation), and with *Rhizopogon pseudorosaeolus* and *Thelephora terrestris* at lower altitudes and distances. Twelve ECM fungal OTUs were found in grasslands and 34 were detected in the pine plantation. Although richness and abundance of ECM fungi decreased with increasing distance from the pine plantation, there was at least one non-native ECM fungal species present in each sampling site, even at 2700 masl and 9000 m distance from the closest plantation. This study provides evidence that the availability of suitable fungal symbionts might constrain but not hinder the expansion of a pine species over wide distances and altitudinal zones even in areas with no native ECM fungi.

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1. Introduction

Biological invasions are recognized as a major threat to biodiversity (Sala et al., 2000). The mechanisms behind non-native plant expansion on an exotic range have been shown to be complex and variable across ecosystems (Levine et al., 2003).

The altitudinal expansion of non-native species over high elevation environments is gaining interest in the last decade and is increasingly documented in the literature (e.g. McDougall et al., 2011; Alexander et al., 2011; Pollnac and Rew, 2014; Tecco et al., 2016). It was recently shown that non-native species with broad climatic tolerances, rather than specialized stress tolerants, are capable of expanding from low to high elevations along the corridors of introduction (Alexander et al., 2011; Tecco et al., 2016). This broad climatic tolerance combined with enough residence time in the region (e.g. Haider et al., 2010; Pyšek et al., 2011) may underlie the success of non-native species at high elevational ranges.

Many plant species form obligatory symbiotic interactions, such as mycorrhizas, to establish, grow, and reproduce (Smith and Read, 2008). Therefore, most exotic plant species also need to rely on compatible belowground mutualists in their new environments (Nuñez and Dickie, 2014). For these plants, three major strategies have been proposed (Dickie et al., 2010): (a) those that can establish symbiosis with the native organisms in the invasive range (novel mutualisms), (b) those that establish symbioses with native organisms that are also native to the home range of the invasive plant (cosmopolitan mutualisms), and (c) those that establish symbioses with invasive organisms (co-invaders).

Pines are globally distributed woody invaders (Richardson, 2006; Rejmánek and Richardson, 2013). They establish obligatory symbioses with ectomycorrhizal (ECM) fungi and cannot establish and survive for long periods without them (Allen, 1991). Therefore, both symbionts, the pine and the fungi, need to co-invade in habitats in which compatible ECM fungal symbionts are absent in native plant communities. It is now well documented that both pines and ECM fungi are able to disperse or escape from plantations and to get co-established in pine-free habitats (e.g. Dickie et al., 2010; Hayward et al., 2015a, 2015b; Hynson et al., 2013; Nuñez

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et al., 2009, 2013; Salgado Salomón et al., 2011). However, the evidence is restricted to horizontal expansion (i.e. similar altitudes) and short distances from the plantations (i.e. ≤ 1000 m). It is not known whether pines and ECM fungi can co-occur and survive outside plantations at longer distances and elevations in which they might be constrained by climate conditions and/or dispersal limitations. Moreover, previous studies on pine expansion have identified those fungal species that colonize pine roots, but did not provide evidence on the complete pool of ECM fungi that can disperse over considerable distances and provide suitable conditions for the invasion front of pines. In other words, we do not know their capabilities to expand to altitudinal zones in which they currently are not present.

Despite the traditional belief that mountains are less prone to invasions than other ecosystems, there is increasing attention to the expansion of alien species over high elevation environments (e.g. Pauchard et al., 2009). In central Argentina, the Sierras de Córdoba mountain range includes a wide elevational gradient (500–2790 m asl) that is threatened by an incipient spread of woody alien species from lower altitudes (Giorgis et al., 2011). Extensive plantations of *Pinus elliottii* were established in the lower belts of these mountain ranges. In certain areas, some individuals have already escaped from plantations and have expanded to higher altitudes, but not above 1850 m asl (Giorgis et al., 2011). In these ecosystems there are no native ECM host plants.

Expansion of woody aliens over altitudinal ranges has been poorly studied in comparison to other growth forms such as herbs (McDougall et al., 2011). Moreover, most of the evidence on the occurrence of non-native flora along elevational gradients comes from species that are already established in their non-native ranges. However, current altitudinal limits of plant distribution may not necessarily reflect their actual climatic tolerance (Araújo and Pearson, 2005; Tecco et al., 2016). This could be the case of *P. elliottii*, i.e. we cannot currently predict if climatic factors and/or lack of compatible fungal symbionts (e.g. Peay et al., 2012) will constrain their expansion to more distant areas and higher altitudes where they currently are absent. For this reason, we combined field experiments with glasshouse essays and DNA metabarcoding analysis of soil samples taken along an altitudinal gradient that is threatened by an incipient spread of exotic *Pinus elliottii* to assess: (a) if pines can survive and form ectomycorrhizas at elevations outside of their current range and (b) which fungal partners are present in soils at different altitudes (900–2700 m asl) involving long distances from plantations (i.e. 100–9000 m).

2. Materials and methods

2.1. Study site

The study was conducted in the Sierras Grandes mountain range in central Argentina. The experimental plots were placed along an altitudinal gradient ranging from 900 m asl to 2700 m asl (Linderos road, 32° 50'S, 64° 90'W), near the highest peak of the mountain range. The gradient comprises the following vegetation belts described by Cabrera (1976) for the Mountain Chaco District: (1) the upper portion of Chaco mountain woodlands, which is distributed from 400 to 1300 m asl; (2) an intermediate belt devoid of forest currently occupied by mountain grasslands and shrublands (1300–1700 m asl); and (3) a mosaic of high mountain grasslands and *Polylepis australis* (Rosaceae) woodlands (above 1700 m asl). There are no ectomycorrhizal species in these ecosystems. Along the gradient, temperatures vary from temperate-warm to temperate-cold. Specifically, mean annual temperature at the lower end of the gradient (900 m asl) is 15.7 °C dropping to 7.4 °C near the summit at 2700 m asl (Marcora et al., 2008). There is

no frost-free period over the 1800 m asl. Mean annual precipitation varies between 750 and 970 mm, with most rainfall concentrated in the warmer months, from October to April (Cabido, 1985; Colladon et al., 2010). The main economic activity is livestock rearing that had begun in the early 17th century and had completely replaced the native herbivore (*Lama guanicoe*) by the beginning of the 20th century (Díaz et al., 1994).

2.2. Study species

Pinus elliottii (slash pine) is native to the southeastern United States. The rainfall in its native range averages about 1270 mm and is concentrated mainly in the warmer period. The mean annual temperature in the slash pine region is 17 °C (Burns and Honkala, 1990).

Together with other *Pinus* species, it was introduced to central Argentina in the 1960s (Ferchmin, 1969) where it now reproduces and expands naturally (Giorgis and Tecco, 2014). In the sampling region, several ECM fungi have been observed to fruit in *P. elliottii* plantations, such as *Endogone* sp., *Rhizopogon* spp., *Inocybe* sp., *Paxillus* sp., *Scleroderma* spp., *Suillus* spp., *Amanita muscaria*, and *Thelephora terrestris* (Nouhra, 1999; Nouhra et al., 2008, 2012; pers. obs.).

2.3. Experimental design

We transplanted seedlings and tested their survival along the contrasting environmental conditions that characterize the altitudinal gradient. The field experiment was complemented with glasshouse assay evaluating whether soils from different altitudes contained mycorrhizal inocula to colonize roots.

Four sites were selected along the altitudinal gradient, placed at intervals of c. 400–600 m asl (965, 1600, 2248, and 2685 m asl). All sites were grasslands established on ridges with similar gentle slopes and high solar insolation (see Tecco et al., 2016 for more details). At each altitudinal site, three plots (4 × 4 m) were selected within a livestock enclosure. These sites were established at a distance of c. 110, 3000, 6000, and 9000 m, respectively, from the closest pine plantation. We cannot discard the occurrence of some scattered pine seedlings in between the plots and the plantations but they would not be a significant source of fungal propagules in comparison with the thousands of hectares of mature pine plantations. Moreover, pines are absent above 1850 m asl (Giorgis et al., 2011). For simplicity, altitudinal sites will be hereafter referred as: 900, 1600, 2200, and 2700 m asl.

2.4. Seedling production

Seeds were provided by the Instituto Nacional de Tecnología Agropecuaria Montecarlo (Misiones, Argentina). The seeds were surface sterilized with 10% sodium hypochlorite for 10 min, submerged in water for 24 h and then stored at 4 °C for 45 d. Then, they were germinated in a glasshouse in an autoclaved mix of sand and native soil (2:1 v v⁻¹). After 20–25 d, these seedlings were used for glasshouse and field experiments.

2.5. Glasshouse experiment

Seedlings were transplanted at the same time to 48 pots (500 cm³). All pots contained 450 ml of autoclaved mix of sand and native soil (2:1 v v⁻¹). Soil suspensions from each altitude were used as soil inocula. We diluted a soil fraction in sterile water (1:5 v v⁻¹) and added 40 ml of this solution to six pots. In the same way, a sterilized soil fraction was diluted in sterile water and 40 ml of this solution was added to another six pots as control for possible

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