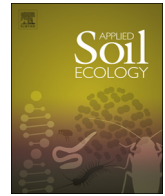




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## Co-invasion of ectomycorrhizal fungi in the Brazilian Pampa biome

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### ABSTRACT

The introduction of ectomycorrhizal fungi along with the introduced ectomycorrhizal plants is rarely considered at the ecosystem level. In Brazil, the Pampa biome is the dominant ecosystem in the Rio Grande do Sul State, predominantly with pastoral management but intensively planted with non-native trees over the last century. Sporocarps of ectomycorrhizal and putative ectomycorrhizal fungi were collected in Pampa biome native forest vegetation and plantation forests during the period 2009–2013, with an emphasis on plantations of eucalypts and pines. Morphological analysis and molecular markers were used to identify collected sporocarps. A total of 60 different taxa were collected, mainly fitting into Australasian ectomycorrhizal fungi lineages. Among collections, two turned out to be saprotrophic species from *Amanita* belonging to the subsect. *Vittadiniae*. The ectomycorrhizal fungi reported here showed that some co-introduced lineages are frequent co-invaders in the Brazilian Pampa biome with alien ectomycorrhizal trees, especially *Descolea*, *Hysterangium*, *Laccaria*, *Pisolithus-scleroderma* lineages. No ectomycorrhizal sporocarps were found in either plantation forest or in native forest sites and no novel associations were observed between native ectomycorrhizal fungal species and introduced plants. All ectomycorrhizal fungi co-introduced in the Brazilian Pampa were recorded with plant species of Australian or North American origin. The study has raised additional questions regarding the distribution, ecology and taxonomy of fungi from the Brazilian Pampa biome.

### 1. Introduction

The Brazilian Pampa biome is part of the larger Pampa area covering the southern half of the Brazilian state of Rio Grande do Sul, Uruguay and several N and NE provinces in Argentina. In Rio Grande do Sul, it has important agricultural and economic potential as it covers over 60% of the total area of the state (Boldrini et al., 2010; IBGE, 2016). Traditional uses of land in the Pampa biome are for extensive pastures and agriculture; however, there has been a 26% decrease in natural pastures in the Brazilian Pampa biome since 1975 due to intensive agricultural activities and forest plantations (de Oliveira et al., 2017). The majority of forested areas were planted with alien forest species, mainly commercial plantations of *Eucalyptus* spp. and *Pinus* spp. These anthropogenic activities have been causing severe ecosystem changes due to the water and fertilization regimes, desertification of plantation areas, sedimentation of bodies of water in the surrounding lowlands, and excessive use of herbicides (ARBA, 2007).

The Pampa biome environmental conditions are suitable not only for setting up plantations and intensive production of alien forest tree biomass, but also for co-occurring ectomycorrhizal fungi, since the climate in the Pampa biome is warm, with precipitation of 600–1200 mm/year, evenly distributed through the year (Overbeck et al., 2006), making it a suitable place for a center of origin of introducing ectomycorrhizal trees and their symbiotic fungi. The soil in the Brazilian Pampa was formed from sedimentary silicate or carbonate rocks, and frequently has an extremely sandy texture that makes it fragile, prone to erosion and poorly retains water (Roesch et al., 2009).

Besides favorable climate conditions, there are other factors that influence invasion by plants, but these remain poorly understood. One of the mechanisms related to successful co-invasion of plants with ectomycorrhizal fungi is compatibility in symbiosis (Nuñez et al., 2009, 2013; Dickie et al. 2017), as biological invasions can be facilitated by compatible ectomycorrhizal species (Díez, 2005). The evaluation of such a correlation first requires a diversity study within plantation

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forests. Some plants, such as pines, have turned in aggressive invasive species spreading outside planted areas in the southern hemisphere, with millions of hectares invaded (Simberloff et al., 2010). As recently observed, those pines carry their ectomycorrhizal partners from areas of origin thus spreading them outside the plantation areas (Sulzbacher et al., 2016). Also, ectomycorrhizal fungi themselves are increasingly being recognized as invasive species (Dickie et al., 2016). On the other hand, ectomycorrhizal fungi can also limit plant invasions, when compatible mycelium is less frequent or cannot adapt to local conditions (Nuñez et al., 2013; Liebhold et al. 2017). Such an effect has not yet been shown for the Pampa biome in Brazil.

Brazil has only recently been more intensively studied for its ectomycorrhizal fungi diversity, both native and introduced (Sulzbacher et al., 2013a,b; Roy et al., 2016; Sulzbacher et al., 2017a). Vellinga et al. (2009) noted the global distribution of introduced ectomycorrhizal fungi and their high diversity for at least 200 species of Basidiomycetes and Ascomycetes which have been moved from their native ranges to novel habitats. The majority of the noted species and their sporocarps were associated with various eucalypts and pines (*ibid.*). The same has been observed by several authors specifically for South America (Garrido, 1986; Dunstan et al., 1998; Nouhra et al., 2008; Nuñez et al., 2013). However, it remains an open question as to whether their propagules are disseminated to adjacent (native or introduced) forests, as well as whether they can be established and persist in new areas (Pringle et al., 2009). There is a significant lack of information regarding the presence and diversity of introduced ectomycorrhizal fungi as well their ecological and biogeographic patterns not only for South America but also for most other continents.

Due to its environmental, economic, and agricultural significance, the Pampa biome in Brazil has been the focus of several theoretical and applied studies that have studied the diversity and distribution of ectomycorrhizal fungi principally associated with exotic forest trees as well as among other taxonomic groups. To clarify the presence, geographic range of alien ectomycorrhizal species and their potential invasiveness outside exotic plantations, a meta-analysis of the ectomycorrhizal fungi from the Brazilian Pampa biome was conducted. We applied a phylogenetic approach in order to discover the distribution, roles and potential origin of individual species or haplotypes. In particular, we targeted mature sporocarps of epigeous and hypogeous ectomycorrhizal fungi as the source of spores and potential for their dissemination. For covering potential sources and invaded areas by ectomycorrhizal fungi we focused on plantation forests, invasive forest trees outside plantation sites, and on native forest/woody vegetation in the Pampa biome area.

## 2. Materials and methods

### 2.1. Exotic plantations in the Pampa biome

The Pampa biome is primarily a productive pasture area covering vast areas of the state of Rio Grande do Sul (Brazil). The Pampa biome variety of soil classes, in areas of sampling predominantly Orthents (classified as Neossolo Litólico and Neossolo Regolítico in the Brazilian Soil Taxonomy), Udoll soils (Chernossolos) and the Uderts (Vertissolos) (Streck et al., 2008; Roesch et al., 2009). Large-scale exotic tree plantations have been established in the Pampa biome since 1950, currently covering over 443,000 ha of plantations of various ages (Couto et al., 2011). Most plantations are monodominant sites of *Eucalyptus dunnii* Maiden, *E. grandis* Will ex Maiden, *Pinus elliottii* Little and Dorman or *P. taeda* L. that in some places already occur mixed with native vegetation (Roesch et al., 2009). This study focused on both the mature plantations of pines and eucalypts and the invaded sites with natural vegetation mixed with the introduced trees. Other small-scale plantations of *Acacia*, *Carya*, etc. exist but were not considered; two native sites, where no invasive trees were observed, were selected as control plots. Surveys were performed in the two designated areas, where all

sporocarps were collected for comparison. The area of Espinilho State Park is situated within the longitudes 57° W and 58° W and latitudes 30° S and 31° S at the Brazilian border with Argentina. The dominant vegetation in this park is *Prosopis algarobilla* Gris., *Prosopis affinis* Spreng. and *Vachellia caven* (Molina) Seigler & Ebinger. We also sampled fungi in the Guaritas Reserve, located at 30° 30' 43" S, 53° 29' 27" W, in the Serra do Sudeste region. The predominant native vegetation is *Allophylus edulis* (A.St.-Hil., Cambess. & A. Juss.) Radlk., *Casearia sylvestris* Sw., *Dyckia maritima* Baker, *Erythrina cristagalli* L., *Eugenia uniflora* L., *Ficus luschnathiana* (Miq.) Miq., *Mimosa rocae* Lor. & Niederl., *Parodia ottonis* (Lehm.) N. P. Taylor and *Sebastiania commersoniana* (Baillon) Smith & Downs.

### 2.2. Collection of fungi

Epigeous and hypogeous sporocarps of putative ectomycorrhizal fungi were collected at different times throughout the year. Mycological surveys took place at 15 plantations in the Pampa biome in the state of Rio Grande do Sul, Brazil (Appendix 1). We also visited two well-preserved Pampean environments with native flora (the Espinilho Park and Guaritas Reserve). Sporocarps were collected using a purposive sampling approach to survey for epigeous and hypogeous sporocarps as described by Miller and Miller (1988) and Castellano et al. (2004). At each site a total survey in order to count the epigeous and hypogeous fungi covered a minimum of 1000 m<sup>2</sup>. Records were retrieved from recent publications and where reference material existed, it was also included in the analysis.

All sporocarps were initially assigned to family and further identified to the genus or species level based on the available literature (Singer, 1986; Pegler, 1997; Montecchi and Sarasini, 2000). Prior to storage all new collections were dried in a forced-air fruit drier with temperature not exceeding 40 °C. All collections are deposited in the fungal collections at the Herbarium of Universidade Federal do Rio Grande do Norte (UFRN), and at the Santa Maria Department of Biology Herbarium (SMDB) of Universidade Federal de Santa Maria (UFSM) under accession numbers (Appendix 1).

### 2.3. Molecular analysis

Representative samples from the genera not previously characterized using a DNA approach were selected for molecular analysis. Genomic DNA was isolated from a fraction of an inner part of the mature sporocarp and then stored at -20 °C in CTAB (Gardes and Bruns, 1993). Total DNA was extracted with the DNeasy® Plant Mini Kit (Qiagen, São Paulo, Brazil). The ITS1-5.8S-ITS2 fragment of nrDNA region was amplified by PCR using ITS1 and ITS4 primers (White et al., 1990). The amplification reaction of the nrDNA fragments was performed according to Baldoni et al. (2012), followed by electrophoresis in 1.5% agarose gel, stained with BlueGreen Loading Dye I® (LGC Biotechnology, Cotia, Brazil) and observed under UV light to confirm a successful amplification of the target DNA fragment. The PCR products mixture were purified directly with the GenElute PCR Clean-up Kit® (Sigma, St. Louis, USA) kit, following the manufacturer's instructions. Sequencing of purified DNA was performed in the ABI PRISM 3100 Genetic Analyzer (Applied Biosystems, California, USA). Sequences were analyzed with the Staden Package 2.0.0b software (Staden et al., 2003) and deposited in GenBank (Appendix 1). BLAST analysis (Altschul et al., 1990) was performed to observe similarities with other sequences deposited in nucleotide databases and to fit unknown sequences in an adequate genus using GenBank database (<http://www.ncbi.nlm.nih.gov/genbank/>). The phylogenetic position of sequences within genera was assessed comparing sequences to representative complete ITS sequences selected from the International Nucleotide Sequence Database Collaboration. A stand-alone freeware version of the MAFFT software (<http://align.bmr.kyushu-u.ac.jp/mafft/software/>) was used for a multiple sequence alignment within a selected genus

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