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What happens to the mycorrhizal communities of native and exotic seedlings when *Pseudotsuga menziesii* invades Nothofagaceae forests in Patagonia, Argentina?

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ABSTRACT

Pseudotsuga menziesii is one of the most widely planted conifers in the Patagonian Andes of Argentina, having invading characteristics that are broadly reported. We studied the mycorrhizal status of seedlings along six Nothofagaceae + *P. menziesii* invasion matrices to investigate their role in the invasive process, according to these hypothesis: a) The abundance and richness of EM will be higher in seedlings grown in their own soil; b) In the presence of native EM inoculum, the invasive plant will be associated with generalist mycorrhizae (EM and/or AM), c) AM associations will be more abundant in *P. menziesii* seedlings grown in Interface or native forest soils, d) Mycorrhizal community differences between treatments will alter host fitness (growth and nutritional parameters). Seedlings from *Nothofagus dombeyi*, *N. antarctica*, *Lophozonia alpina*, *L. obliqua* and *Pseudotsuga menziesii* were set up in a soil-bioassay that included soils from non-invaded Nothofagaceae forests, pure *P. menziesii* plantations, and the interface between both. *Pseudotsuga menziesii* seedlings showed a decreasing, although never null, ectomycorrhizal (EM) colonization pattern from plantations to non-invaded forests, mainly with exotic EM species. *Hebeloma mesophaeum* and *Wilcoxina* sp. 1, two EM species with cosmopolitan distribution, were found to be shared by both tree species. *Hebeloma hiemale* and *Wilcoxina* sp. 1, common mycorrhizal partners of *P. menziesii* in Patagonia although not registered from Nothofagaceae forest, were found to be associated with *N. antarctica*, being the first report for both fungal species. *Pseudotsuga menziesii* seedlings showed the ability to form different arbuscular mycorrhiza (AM) colonization types (*Paris*-, *Arum*-, Both- and Intermediate-types) depending on the treatments, with significantly higher presence of Intermediate-type in the Interface treatment, where colonization was low. The shared EM species and the presence of different AM colonization types imply enhanced possibilities for invasive *P. menziesii* seedlings establishment and development. Seedling features and EM colonization rates evidenced that *P. menziesii* invasion could produce maladaptation (defined as a relative decline in host fitness due to altered mycorrhizal communities from native settings) of mycorrhizal communities, seriously injuring native ecosystem.

1. Introduction

One of the most perplexing questions of ecology is how some plants, when moved or introduced to new areas for productive purposes, can surpass the development of native species and be more abundant than in their natural range (Blossey and Nötzold, 1995; Elton, 1958; Hierro et al., 2005). Given the facts that the majority of plants depend at least on one fungal mutualism (Brundrett, 2009; Núñez and Dickie, 2014), and mutualistic interactions can prevent or facilitate biological invasions (Richardson et al., 2008; Núñez et al., 2009; Spence et al., 2011), a better understanding of invasion on plant communities requires a consideration of the role of fungal partner(s) in the symbiosis (Schnoor et al., 2011).

During the last decade several authors have warned about the invasive capability of *Pseudotsuga menziesii* (Mirb.) Blanco in native Nothofagaceae forests in Patagonia, Argentina (Núñez et al., 2009;

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Table 1
Sampling sites, with indication of matrix type, maximum effective recruitment distance (ERD), transect length, main understory species and sites features.

Sites	GPS point	Matrix type	ERD (m)/ Transect length (m)	Understory species[a]	Treatment	AM SD[b]	AP[c]	MT[d]	SpH[e]	OM[f]	PC[g]	TN[h]	ST[i]	EC[j]	CaC[k]	MgC[l]	KC[m]	NaC[n]
Corcovado	Lat.: −43.63,	*P. menziesii - N.*	55/235	COSP, SCPA, LOHI, FAIM, MACH, CYSC, RUAC,	Forest	16	810	9	5.81	18.5	21	0.43	Sandy loam	0.09	6.80	3.00	0.30	1.30
	Long.: −71.44	*antarctica*		ACPI, ACSP, POLI, POLA, HOSP, FRCH, OSCH,	Interface	18	810	9	6.49	13.6	33	0.66	Sandy loam	0.20	4.50	6.25	0.53	1.00
				OBAN, RUAD.	Plantation	50.8	810	9	5.80	14.9	23	0.33	Loamy sand	0.08	9.30	1.00	0.40	1.00
Foyel	Lat.: −41.67,	*P. menziesii - N.*	86.4/266.4	SCPA, LOHI, MABO, MACH, CHCU, MUHA, VISP,	Forest	19.6	1490	9.58	5.87	21.7	25	0.82	Sandy loam	0.14	14.30	6.80	0.80	0.90
	Long.: −71.45	*antarctica*		FRCH, BEBU, MUDE, POLI, POLA, FEAR, BRAU,	Interface	26	1490	9.58	6.49	12.2	34	0.47	Sandy loam	0.11	16.00	7.50	0.91	0.80
				OSCH, ACPI.	Plantation	24.4	1490	9.58	5.94	19.6	20	0.75	Loamy	0.08	17.80	9.80	0.60	0.90
ENFORSA	Lat.: −41.23,	*P. menziesii - N.*	78.2/258.2	SCPA, MACH, LOHI, EMCO, BEBU, OSCH, POLI,	Forest	18	1490	9.58	5.26	17.1	18	0.67	Sandy loam	0.14	11.80	7.80	1.00	1.10
	Long.: −71.42	*antarctica*		POLA, FEAR, BRAU, FRCH, VISP., MUDE, PLLA,	Interface	21.6	1490	9.58	5.13	17.4	31	1.02	Sandy loam	0.18	8.75	5.75	0.51	0.90
				RUAD, MUHA, ACPI, TRRE.	Plantation	49.6	1490	9.58	5.52	10.6	13	0.30	Sandy loam	0.06	16.30	8.30	0.80	0.90
Isla Victoria	Lat.: −40.97,	*P. menziesii - N.*	218.6/398.6	BEBU, RUAD, MACH, VISP, MUHA, SCPA, ARCH,	Forest	8.8	1544	8.68	6.32	9.6	22	0.32	Sandy loam	0.04	10.80	5.30	0.40	1.00
	Long.: −71.53	*dombeyi*		LOHI, AUCH, LUAP, CHCU, MUDE, POLI, POLA,	Interface	4.4	1544	8.68	6.07	12.9	35	0.46	Sandy loam	0.09	14.75	6.00	0.76	0.90
				FEAR, BRAU, ROEG.	Plantation	16.4	1544	8.68	5.75	14.7	26	0.28	Sandy loam	0.14	12.50	4.80	0.50	1.30
Est. Quechuquina	Lat.: −40.15,	*P. menziesii - L.*	44.61/224.61	CHCU, MACH, ARCH, MUHA, TAOF, SCPA, POLI,	Forest	18	1834	12.2	5.17	16.1	22	0.36	Sandy loam	0.44	9.80	3.50	0.40	2.10
	Long.: −71.59	*alpina - L. obliqua*		POLA, FEAR, BRAU, TRRE, OSCH, FRCH, CATH,	Interface	15.2	1834	12.2	5.67	13.1	29	0.62	Sandy loam	0.19	8.00	6.75	0.43	0.60
				CIVU, ALAU, RUAD, BEBU, RUAC, AUCH, MOPE.	Plantation	25.6	1834	12.2	5.5	13.2	37	0.33	Sandy loam	0.26	12.00	7.00	0.50	1.80
Est. Newmeyer	Lat.: −40.12,	*P. menziesii - N.*	19/199	CHCU, SOAC, SASP, PRCE, MACH, LOHI, MUHA,	Forest	21.6	2258	12.2	5.7	26.5	33	0.54	Sandy loam	0.32	22.30	11.30	0.70	1.90
	Long.: −71.32	*dombeyi*		OSCH, RUAD, POLI, POLA, FEAR, BRAU.	Interface	20	2258	12.2	5.57	8.25	35	0.31	Sandy loam	0.24	12.50	5.25	1.03	0.90
					Plantation	19.2	2258	12.2	6.79	9.8	12	0.28	Loamy sand	0.08	17.50	2.30	0.20	1.20

[a] *Understory species:* ACPI: *Acaena pinnatifida;* ACSP: *A. splendens;* ALUA: *Alstroemeria aurea;* ARCH: *Aristotelia chilensis;* AUCH: *Austrocedrus chilensis;* BEBU: *Berberis buxifolia;* BRAU: *Bromus auleticus;* CATH: *Carduus thoerneri;* CHCU: *Chusquea culeou;* CIVU: *Cirsium vulgare;* COSP: *Colletia spinossisima;* CYSC: *Cytisus scoparius;* EMCO: *Embothrium coccineum;* FAIM: *Fabiana imbricata;* FEAR: *Festuca argentina;* FRCH: *Fragaria chiloensis;* HOSP: *Hordeum* sp.; LOHI: *Lomatia hirsuta;* LUAP: *Luma apiculata;* MABO: *Maytenus boaria;* MACH: *M. chubutensis;* MOPE: *Montia perfoliata;* MUDE: *Muticia decurrens;* MUHA: *Muehlenbeckia hastulata;* OBAN: *Obidia andina;* OSCH: *Osmorrhiza chilensis;* POLA: *Poa lanuginosa;* POLI: *P. ligulata;* PLLA: *Plantago lanceolata;* PRCE: *Prunus cereseae;* ROEG: *Rosa eglanteria;* RUAC: *Rumex acetosella;* RUAD: *Ruhmora adiantiformis;* SASP: *Sambucus* sp.; SCPA: *Schinus patagonicus;* SOAC: *Sorbus acuaiparia;* TAOF: *Taraxacum officinale;* TRRE: *Trifolium repens;* VISP: *Vicia* sp.

[b] AM SD: AM spore density (spores/100 gr. Of dry soil).

[c] *AP: annual precipitation (mm).*

[d] MT: mean temperature (°C).

[e] SpH: soil pH.

[f] OM: organic matter (%).

[g] PC: soil phosphorous content (mg/kg of soil).

[h] TN: total soil nitrogen content (%).

[i] ST: soil texture.

[j] EC: Electrical conductivity (ds/m).

[k] Calcium content (meq/100 g).

[l] Magnesium content (meq/100 g).

[m] Potassium content (meq/100 g).

[n] Sodium content (meq/100 g).