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Effect of *Pinus contorta* invasion on forest fuel properties and its potential implications on the fire regime of *Araucaria araucana* and *Nothofagus antarctica* forests

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The effect of a pine invasion on the fuel Abstract characteristics was studied to predict fire behaviour and hypothesize potential changes on fire regime. Subalpine Andean forests, fire-prone environments, in the Malalcahuello Reserve in south-central Chile were invaded by the non-native Pinus contorta affecting the native endangered trees Araucaria araucana and Nothofagus antarctica communities. Several fuel components were evaluated by studying different variables, such as fuel load, vertical and horizontal continuity, and flammability of native and invasive tree species. The survey was conducted in five stand conditions: A. araucana and N. antarctica stands, each with and without invasion of P. contorta, and stands with only P. contorta (invasion source). The invasion of P. contorta increased the vertical fuel continuity in the Araucaria forest. The flammability analysis showed that P. contorta is a species highly flammable in comparison to the native trees. The invasion of P. contorta in the Malalcahuello Reserve is under progression and if the process of invasion continues the effects on fuel characteristics will increase. These results suggest that wildfires will be more intense and severe, and that the type of fires of the Malalcahuello Reserve will change from a mixed fire regime to a crown fire regime. These changes will affect plant regeneration, and a positive feedback that favours the *P. contorta* invasion could emerge. Long-term studies to understand the effect of invasive woody plants on the fire regime are essential for the control of these invasions, especially for the conservation of biodiversity and ecosystem processes in the *Araucaria– Nothofagus* ecosystems is the Chilean and Argentinean Patagonia.

Keywords Pine invasion · Fuel load · Flammability · Fuel continuity · Woody plant invasion · Fire ecology

Introduction

In ecosystems with natural fire dynamics the composition of plant communities and their fire regime are inherently related. Invasive plants that arrive in these ecosystems are supposed to play an important role in modifying the fire regime by affecting the fuel properties (Brooks et al. 2004; Mandle et al. 2011). Fuel is an important component of fire regimes, related by positive feedback through ecosystem properties and plant composition. Changes in fuel can alter fire behaviour, plants composition, and structure of the ecosystem, and in the long term modify the fire regime in an invaded area (Brooks et al. 2004). Invasive plants

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modify fuel through changes in fuel load, phenology of plants by altering light availability, flammability by volatile chemicals, and a new spatial arrangement of fuel (Dibble and Rees 2005). Most of the information of the effects of invasive plants on fire regime is shown from studies of invasive grasses, showing that increases on fuel biomass and horizontal continuity enhance the frequency of fire (D'Antonio et al. 2000; Platt and Gottschalk 2001; Brooks and Pyke 2002; Brooks et al. 2004; Mandle et al. 2011). Few studies on invasive woody plants showed decrease or inhibition of fire (Brooks et al. 2004) while others report an increase in frequency and intensity of fire (García et al. 2013). This relationship between fire and invasive woody plants is not fully understood, and it depends on the characteristics of the invasive species and the affected habitat (Mandle et al. 2011).

Over the last decades, increasing evidence has confirmed that the genus Pinus comprises some of the most invasive tree species. At least 19 species have been recognized for invading natural ecosystems in the southern hemisphere, eight of which were considered to cause major problems due to their invasive capacity (Pinus halepensis Mill., Pinus patula Schltdl. & Cham., Pinus pinaster Aiton, Pinus radiata D.Don, Pinus contorta Douglas ex Loudon, Pinus nigra Arnold, Pinus ponderosa P. Lawson & C. Lawson and Pinus sylvestris L.) (Richardson 1998). Several attributes have been identified as promoters of their invasiveness, including a high seed production, small seeds size, short juvenile period, and a short interval of seed production (Richardson et al. 1994; Rejmánek and Richardson 1996). These attributes help Pinus spp. populations to persist and expand in habitats with frequent disturbance regimes (Richardson et al. 1994).

Disturbance events like wildfires enhance the invasion of pines, because many species are distributed on fire-prone habitats, ranging from environments favouring frequent understory or surface fires to sites subject to less frequent but high intensity crown fires (Keeley 2012). Pines have evolved in association with fire as an ecological process, promoting the dominance of fire adaptations (Keeley et al. 2011; Keeley 2012). Fire-adaptive traits include bark thickness, self-pruning, resprouting, flammability, serotinous cones, and germination triggered by smoke, ashes and heat-shock (Kimmins 1987; Bond and Midgley 1995; Pyne et al. 1996; Bond and Keeley 2005; Keeley et al. 2011). The relationship between fire and pine invasions have been studied in the fynbos ecosystem in South Africa, where invasive pines, e.g. *P. halepensis*, *P. radiata*, and *P. pinaster*, showed rapid population growth after fire (Richardson 1988). However, evidence remains scarce on the effects of pines in fire regimes in other regions of the globe.

In order to understand the effects of the presence of an invasive pine as a new element in an ecosystem, it is necessary to know the properties of native and exotic fuels. These effects have to be evaluated at two levels, on changes in the ecosystem, and on differences in the fuel characteristics between native and invasive species. The aim of this research was to determine the effects of the exotic woody plant Lodgepole pine (Pinus contorta) on the fuel characteristics in the Malalcahuello National Reserve in south-central Chile (hereinafter "Malalcahuello Reserve"). This exotic species is considered one of the most invasive species in the world (Richardson et al. 1994; Rejmánek and Richardson 1996; Richardson 1998; Ledgard 2001; Peña et al. 2007; Simberloff et al. 2010). Countries affected by P. contorta include Argentina, Australia, Ireland, New Zealand, Sweden, United Kingdom, and Chile (Richardson et al. 1994; Rejmánek and Richardson 1996; Despain 2001; Ledgard 2001; Richardson and Rejmánek 2004; Sarasola et al. 2006; Peña et al. 2008; Langdon et al. 2010; Simberloff et al. 2010). In the Malalcahuello Reserve (Chile) this species is currently invading more than 78 ha of native forest of the endangered species Araucaria (Araucaria araucana (Molina) K.Koch) and Ñirre (Nothofagus antarctica (G.Forst.) Oerst.) (Peña et al. 2007, 2008). Here, the following questions are addressed: (1) Which are the changes that the invasion of *P. contorta* causes on fuel load, and on vertical and horizontal fuel continuity in the native forest?; (2) What are the differences of fuel flammability between the exotic (P. contorta) and the native tree species (A. araucana and N. antarctica)?; (3) What are the potential implications of P. contorta invasion for the fire regime in the A. araucana-N. antarctica forest ecosystems?

Methods

Study species

Pinus contorta is native to the northwest of North America. Its natural range covers parts of Canada and

the United States (Klinka 2002). Growing up to 35 m in height and up to 60 cm in diameter at breast height (DBH), it is a pioneer, shade intolerant tree of rapid growth that grows in relatively poor sites (Kral 1993; Lotan and Critchfield 1990; Ledgard 2001; Klinka 2002). *Pinus contorta* is known by its wide ecological amplitude and tolerance, growing from sea level to 3,660 m a.s.l. Considering the large geographical distribution, minimum tolerable temperatures range from -57 to 7 °C, and maximum temperatures from 27 to 38 °C. Annual precipitation varies between 250 and 500 mm (Lotan and Critchfield 1990).

In its natural range, P. contorta produces viable seeds at an early age between 5 and 10 years. The production of seeds varies within intervals of 1-3 years with hundreds to thousands of seeds per tree. The seeds are small and wind dispersed (Lotan and Critchfield 1990). Germination and establishment are enhanced at full sunlight and on mineral soil (Despain 2001). Pinus contorta is adapted to wildfires by serotinous cones (Muir and Lotan 1985; Kral 1993). Pinus contorta forests are dependent of wildfires with variable fire regimes, ranging from superficial fires of low intensity to crown fires of high intensity. Depending on the site, fire intervals can vary from 100 to 500 years (Brown 1975; Lotan et al. 1985). However, for the Rocky Mountains the fire interval has been determined for less than 100 years (Lotan et al. 1985; Sibold et al. 2006).

Study site

The Malalcahuello Reserve is located in the Araucanía Region (71°28' and 71°35'W; 38°23' and 38°30'S) with an area of 13,730 ha (Fig. 1). The climate is mediterranean humid with a mean annual temperature of 8.5 °C and mean annual precipitations of 3,083 mm and 1-2 dry months per year. Topographically, one of the most outstanding characteristics is the Lonquimay volcano with an altitude of 2,806 m a.s.l.; the mean altitude of the reserve is 1,420 m a.s.l. (Espinosa 1996). The main vegetation formation corresponds to high-Andean A. araucana forests associated with deciduous species, ñirre (N. antarctica) in drier subalpine valleys (1,100-1,200 m a.s.l.) and lenga (Nothofagus pumilo (Poepp. & Endl.) Krasser) at higher altitude (1,200–1,500 m a.s.l.) and more mesic sites: also in more humid sites A. araucana mixed with coigüe (Nothofagus dombeyi (Mirb.) Oerst.). Above 1,400 m a.s.l. the vegetation is dominated by pure *A. araucana* forests with an abundant grass cover (*Festuca scabriuscula* Phil.) and in less proportion by *Nothofagus* species. In mesic forests, an important element in the plant composition of the understory is a native woody bamboo species, *Chusquea culeou* E.Desv. forming dense masses of vegetation (Espinosa 1996; Peña et al. 2008).

In the reserve, there are experimental plantations of P. contorta, P. sylvestris, P. ponderosa and Pseudotsuga menziesii (Mirb.) Franco, established by the Forest Institute (INFOR) in 1970's (Peña et al. 2008). These plantations have not been subject to any silvicultural treatment and currently P. contorta is reported as invasive in the Reserve (Peña et al. 2007, 2008; Langdon et al. 2010). Peña et al. (2008) determined that the invasion of P. contorta is affecting more than 78 ha, initiated from the original plantation of 0.12 ha; the invasion process occurred during a period of 33 years. The natural regeneration of the species had an average density of 1,043 plants ha^{-1} . The average maximum distance at which an individual was found from the seed source was 1.2 km. The invasion process has affected mainly A. araucana-N. antarctica forests, and less under the canopy of other pine species, and within the more dense Nothofagus forests.

The relation of *Araucaria-Nothofagus* forests dynamics with a disturbance regime where wildfires are the most important disturbance is well known, wildfires that can be natural or by anthropogenic causes (Burns 1993; González et al. 2005, 2006, 2010b). The *Araucaria-Nothofagus* forests are strongly influenced by a gradient of mixed severity surface fires up to high severity crown fires (Burns 1993; González et al. 2010b). Silva (2009) determined for *Araucaria-Nothofagus* forests located in a contiguous valley within the Malalcahuello Reserve that at least nine wildfires have occurred during the period from 1898 to 1975, with a high fire recurrence period from 1927 to 1975 and the highest concentration within the 1960's decade.

Sampling design

Fuel load

The survey was conducted in five different stand conditions at the reserve during autumn 2012: (1) *A*.

Fig. 1 Study site. **a** The location of the study site in the Araucanía Region in Chile. **b** The conditions studied and location of the random plots within these conditions (USGS, NASA, NGA 2008)



araucana forests (hereinafter "araucaria condition"), (2) *A. araucana* forests invaded by *P. contorta* ("araucaria-pine condition"), (3) *N. antarctica* forest ("ñirre condition"), (4) *N. antarctica* forest invaded by *P. contorta* ("ñirre-pine condition"), and (5) *P. contorta* invasion (seed source, "pine condition") (Fig. 2). The pine condition is a site invaded by *P. contorta* near the plantations and was originally an open area of the *A. araucana* forest. Each condition was georeferenced by using a geographic information system (GIS). Five 100 m² plots (10 × 10 m) were randomly chosen in each condition (n = 25 plots). All trees (height > 1.5 m) in the plots were recorded, and for each tree it was measured: diameter at breast height (DBH), total height (H), crown diameter (CD), height to crown base (HC), crown length (CL), and cover of each species (C) using the method of Braun-Blanquet (1964). Because *N. antarctica* trees branches into several shoots from the ground, for this species also the number of stems per tree was counted.



Fig. 2 Conditions studied. **a** *A*. *araucana* forest, **b** *A*. *araucana* forest invaded by *P*. *contorta*; **c** *N*. *antarctica* forest; **d** *N*. *antarctica* forest; **d** *N*. *antarctica* forest invaded by *P*. *contorta*. **e** *P*. *contorta* invasion near the seed source

For the shrub and herb layer, two 1 m² (1 \times 1 m) subplots were established in opposite corners of the 100 m^2 plots (n = 50 subplots). For shrubs, herbs, and trees less than 1.5 m height, species cover and mean height were measured in each subplot. The biomass in each subplot was cut and transported to the laboratory for classification in herbs, shrubs and C. culeou. To quantify the debris, four 0.0625 m² (0.25 \times 0.25 m) subplots, were established in each corner of the 100 m² plots. All biomass was collected and separated in litter and downed woody material. The downed woody material was then classified in size classes by average moisture time lag: 1 h (0-0.6 cm diameter) and 10-100 h (0.6-7.5 cm) (Brown 1974). All biomass material classified was dried in ovens at 105 °C until constant weight was reached and then was weighed to obtain dry weight (DW).

To estimate canopy fuel biomass allometric equations were developed. A total of 60 trees were sampled by destructive methods: 20 *P. sylvestris* trees, 20 *P. contorta* trees, and 20 *N. antarctica* shoots. The trees represented the diametric amplitude of the plots surveyed, 4–5 trees per diametric class between 1 and 20 cm DBH were sampled during the summer of 2013. For each tree, measurements of DBH, H, HC, CL, CD and age (by counting growth rings) were taken. The material was weighed in situ and a sample of branches and cross sections of the trunk were taken. The fuel was separated in size classes: foliage + branches <0.6 cm, branches 0.6-2.5, 2.5-7.5 cm and bole (Brown 1974; Scott and Reinhardt 2002; Reinhardt et al. 2006). The fine crown fuel (foliage + branches <0.6 cm) was considered as active fuel (Scott and Reinhardt 2002), except for A. araucana, where only leaves were considered as active crown fuel. The biomass was oven dried at 105 °C until constant weight and then weighed. The dry weight was used to adjust biomass functions based in regression models for fuel components, crown fuel, and total tree biomass (Table 1). The models were selected using indicators of goodness of fit (Segura and Andrade 2008). Fittings of the allometric models were processed using the REG procedure of the statistical analysis software SAS version 9.0. Due to the protection status of A. araucana in Chile, which does not allow its harvesting, available biomass equations for Araucaria angustifolia (Bertol.) Kuntze were used: foliage DW = -67.01 + 4.389 *DBH, branches DW = -137.238 + 7.145 * DBH, trunk DW = $635.374 + 32.302 * DBH^{2}*H$, and total tree $DW = -41.713 + 0.565 * DBH^2$ (Fernández-Tschieder et al. 2008). Araucaria angustifolia is a tree of subtropical to temperate rainforest in Argentina, Uruguay and Brazil (Bittencourt 2007), morphologically similar to A. araucana.

Table 1 Adjusted models for biomass (kg) estimation for N. antarctica, P. contorta and P. sylvestris

Models	Species	п	CF	$R^2_{adj} \\$	F value	Pr > F
Biomass foliage + branches < 0.6 cm						
$\ln(DW) = -2.26 + 0.41 \ln(DBH) + 1.39 \ln(CL)$	N. antarctica	20	1.080	0.81	41.67	< 0.0001
$\ln(DW) = -1.97 + 1.74 \ln(DBH)$	P. contorta	20	1.033	0.96	506.67	< 0.0001
$\ln(DW) = -1.42 + 0.69 \ln(DBH^2)$	P. sylvestris	20	1.066	0.89	146.63	< 0.0001
Biomass branches 0.6–2.5 cm						
$\ln(DW) = -2.34 + 0.91 \ln(DBH \times CL)$	N. antarctica	20	1.093	0.85	109.65	< 0.0001
$\ln(DW) = -4.12 + 2.35 \ln(DBH)$	P. contorta	19	1.385	0.79	67.18	< 0.0001
$\ln(DW) = -3.01 + 1.82 \ln(DBH)$	P. sylvestris	20	1.108	0.89	161.24	< 0.0001
Biomass branches 2.5–7.5 cm ^a						
$\ln(DW) = -5.39 + 5.59 \ln(DBH) - 7 \ln(H) + 3.56 \ln(CL)$	N. antarctica	14	1.384	0.84	24.33	< 0.0001
$\ln(DW) = -7.08 + 1.22 \ln(DBH^2 \times CL)$	P. contorta	12	1.171	0.71	28.28	0.0003
$\ln(DW) = -10.85 + 11.94 \ln(DBH) - 20.56 \ln(H) + 10.77 \ln(CL)$	P. sylvestris	11	1.344	0.86	20.94	0.0007
Crown biomass						
$\ln(DW) = -1.86 + 1.04 \ln(DBH \times CL)$	N. antarctica	20	1.169	0.81	81.93	< 0.0001
$\ln(DW) = -2.18 + 2.09 \ln(DBH)$	P. contorta	20	1.064	0.95	390.02	< 0.0001
$\ln(DW) = -1.31 + 1.56 \ln(DBH)$	P. sylvestris	20	1.102	0.87	123.49	< 0.0001
Total tree biomass						
$\ln(\text{DW}) = -0.8 + 0.62 \ln(\text{DBH}^2 \times \text{CL})$	N. antarctica	20	1.048	0.94	279.96	< 0.0001
$\ln(DW) = -1.74 + 2.16 \ln(DBH)$	P. contorta	20	1.039	0.97	668.14	< 0.0001
$\ln(\text{DW}) = -0.8 + 0.81 \ln(\text{DBH}^2)$	P. sylvestris	20	1.053	0.93	249.81	< 0.0001

CF correction factor (Sprugel 1983), R_{adj}^2 coefficient of determination

^a Fuel present only in trees with DBH >6 cm

Fuel structure sampling

The vertical and horizontal fuel continuity was determined using the data from the plots and subplots. Mean height (H), height to crown base (HC), and mean cover was calculated for each understory component (herbs, shrubs, and *C. culeou*), and the different tree species for each condition. The disruption of the vertical continuity (DVC) was determined by the equation:

DVC = Mean H understory

- mean HC dominant tree species. (1)

Horizontal continuity was evaluated through the accumulative crown area (ACA) of the tree layer through the equation:

ACA =
$$\sum \left[\pi/4 \times (CD_i)^2 \right]$$
 (2)

where, CD_i is the crown diameter for ith tree.

Fuel flammability

The flammability is defined as the capacity of the plants to burn, which can be evaluated by four aspects: ignitability, sustainability, combustibility, and consumability (Anderson 1970; Martin et al. 1994). The following characteristics were used to estimate flammability: foliar moisture content (ignitability), crown bulk density (sustainability), higher calorific value and volatile content (combustibility), and fine fuel proportion (consumability). The analyses were performed for *P. contorta*, *N. antarctica*, *C. culeou* and *A. araucana*. The foliar moisture content (MC) was calculated based on the fresh weight; the analysis was done for 5 samples for each species, and each sample consisted of several leaves of a tree:

$$MC = (fresh weight - dry weight/fresh weight) \times 100.$$
(3)

The higher calorific value and the volatile material content analysis were developed by the ASTM Norms D5865 (ASTM 2001a) and D3175 (ASTM 2001b) on three samples for each species analyzed. Each sample consisted of several leaves of a tree; the leaves were dried at room temperature and grind. One gram from each dried, grind sample material was taken for the analysis.

The proportion of the fuel by size per species was determined with the data of the trees used in the development of the allometric functions. The proportion was calculated as the percentage of the fuel by size classes (foliage + branches <0.6 cm, branches 0.6-2.5, 2.5-7.5 cm) by DBH category. According to Riaño et al. (2004), the crown bulk density (CBD) was determined by the equation:

 $CBD = Fine crown biomass/(CL \times CD^2).$ (4)

Statistical analysis

The fuel load by condition and the fuel flammability by species was analyzed through the generalized linear model procedure (GLM) in the statistical analysis software SAS. The Tukey test was used as a multiple comparison test to determine significant differences between conditions and species ($\alpha = 0.05$). In addition, the homoscedasticity and normality of residuals were verified. For the vertical and horizontal fuel continuity the pairwise t-student test was used to evaluate differences between invaded versus noninvaded conditions, through TTEST procedure in SAS. A GLM analysis was used for comparing the invaded conditions with the plantation. The multiple mean comparison between conditions was developed with the Tukey test ($\alpha = 0.05$).

Results

Site characteristics

The studied ecosystem presented four tree species: *A. araucana* and *N. antarctica* (native trees), *P. contorta* and *P. sylvestris* (exotic invasive trees); the last species was present in considerable lower abundance than *P. contorta*, reason why this study will only focus on the impacts of *P. contorta*. In addition, there were also isolated trees of *P. ponderosa* and *Pseudotsuga menziesii* present outside the plots. In the understory,

shrub species had stunted growth with similar heights to herbs; *C. culeou* was the most important element with greater abundance in this vegetation stratum (Table 2).

Araucaria araucana forest showed a lower tree density but a higher tree cover, compared with the invaded condition. In the understory layer, the A. araucana forest showed a lower shrub cover in the invaded condition (Table 2). Nothofagus antarctica forests were dense and of low height, the species had tortuous and branched stems from the base (mean number of shoots 19.3 \pm 3). The condition ñirre-pine had lower density of N. antarctica compared with the non-invaded condition. In the ñirre-pine condition, P. contorta had a density similar to the density for N. antarctica. The pine condition located near the original plantation, had the highest cover and density for P. contorta compared to the other conditions studied. In this condition both pine species had higher height and DBH in relation with the other invaded conditions (Table 2, Fig. 3).

In all the conditions a high variability in height, DBH, cover and density of trees, primarily for *P. contorta* and *P. sylvestris* was observed, which was reflected in the extreme minimum and maximum values (Table 2). In general, *P. contorta* and *P. sylvestris* were mostly young individuals. Most trees of *P. contorta* were in the range <6.3 cm of diameter and *P. sylvestris* a range <3.8 cm of diameter (Fig. 3). *Pinus contorta* had a mean age of 12.1 ± 0.9 (min: 6, max: 23), and *P. sylvestris* a mean age of 12.26 ± 0.6 (min: 8, max: 16).

Ecosystem differences

Fuel load

In the debris and understory no significant differences in biomass were detected, except for the fine downed woody fuel (twigs <0.6 cm), where the araucaria-pine condition had the lowest value, 551.7 (\pm 213.7) kg ha⁻¹ and ñirre the highest value with 1,930.6 (\pm 307.1) kg ha⁻¹ (F: 2.95, p < 0.05) (Fig 4).

In the tree layer, the araucaria and araucaria-pine condition had 30,517.7 ($\pm 10,427.5$) kg ha⁻¹ and 30,433.8 (± 7966.8) kg ha⁻¹ of fine crown fuel (foliage + branches <0.6 cm), both values were significantly higher (F: 3.41, p < 0.05) in comparison with the other conditions. For this component the pine

Cond.															
V	Layer	Veget.	DBH (cm)			H (m)			Density (No. tree	es ha ⁻¹)		No. shoots	Cover (%)		
V			Mean (SE)	Min	Мах	Mean (SE)	Min	Max	Mean (SE)	Min	Мах	Mean (SE)	Mean (SE)	Min	Max
5	Г	Aa	44.6 (12.5)	2.1	82.76	9.4 (2.2)	1.6	17	220 (73.5)	100	400		34 (8.1)	10	60
	Ŋ	Shrubs				0.3 (0.1)	0.1	0.5					12.8 (3.0)	4.2	19.4
		C_{C}				1.8 (0.2)	1.3	2					14 (7.9)	0	31.3
		Herbs				0.2 (0.02)	0.1	0.3					15.5 (4.5)	9	26.3
API	Т	Aa	41.6 (13.8)	8.1	79.8	8.4 (1.8)	2.53	15.25	280 (91.7)	100	500		27 (8.6)	5	50
		Pc	4.1 (0.9)	0.5	14.6	3.0(0.3)	1.6	7.02	1,120 (432.9)	500	2,800		23 (7.2)	10	50
		Na	1.3(0.3)	2.1	3.2	1.9(0.1)	1.6	2.27	80 (67.6)	0	400		4 (3.4)	0	20
		P_S	2.6 (1.1)	1.5	4.1	2.7 (0.7)	2	5.9	120 (77.5)	0	400		2.2 (1.0)	0	5
	D	Shrubs				0.2 (0.01)	0.1	0.4					6.5 (0.5)	3.1	10
		C_{C}				1.5(0.1)	1.2	1.6					14.3 (7.9)	7.5	31.3
		Herbs				0.2 (0.02)	0.2	0.3					13 (2.2)	5.5	25.6
IN	Н	Na	5.9 (0.8)	0.6	26.2	3.6 (0.4)	1.7	7.7	2,580 (753.3)	1,400	5,500	19.3 (3.0)	53 (7)	40	80
	D	Shrubs				0.2 (0.1)	0.1	0.7					4.9 (0.8)	3.3	7.9
		C_{C}				1.0(0.1)	0.8	1.3					31.5 (8.8)	0	51.3
		Herbs				0.2~(0.1)	0.1	0.5					9.9 (5.9)	0	31.3
IIIN	Т	Pc	3.7 (0.8)	1.1	13	2.8 (0.6)	1.6	11	900 (356.4)	200	2,200		24.6 (9.8)	5	60
		Na	4.9 (1.0)	-	15	3.3 (0.4)	1.6	6.8	960 (310.8)	300	1,800	15.0 (1.5)	40 (7.2)	20	65
		P_S	2.6 (1.2)	1	12.8	3.2 (0.6)	1.7	7.1	160 (135.2)	0	800		1 (0.4)	0	ю
	Ŋ	Shrubs				0.4 (0.02)	0.1	0.6					13.8 (2.3)	5	20
		C_{C}				0.7~(0.1)	0.6	1.4					20.4 (6.4)	0	38.8
		Herbs				0.2 (0.03)	0.1	0.3					8.6(0.8)	7.1	10.9
Р	F	Pc	4.3 (0.5)	0.4	21.2	3.3 (0.2)	1.1	10.75	4,560 (1768.8)	600	10,700		59 (14.1)	15	95
		P_S	11.9 (5.4)	-	25.4	6.8 (2.1)	1.8	11.5	540 (465.4)	0	2,400		7.9 (3.6)	0	20
	D	Shrubs				0.4(0.03)	0.1	0.8					6.6(1.5)	1.3	10
		C_{C}				1.2(0.3)	0.7	1.8					13.3 (10.5)	0	51.3
		Herbs				0.2 (0.02)	0.2	0.3					13.3 (2.9)	6.3	23.1
Cond. cor	dition (2 vis Nat	A: araucari. N antarcti	a, API: araucat	ria-pine,	NI: ñirre, <i>RH</i> diame	NIPI: ñirre-pir ter at breast he	icht H	ne), Laye	r (T: tree, U: under	story), Ve	get.: Vege	tation (Aa: A. a	raucana, Pc: F	. contor	ta, Ps:



Fig. 3 Diameter distribution by tree species for each condition studied. Categories amplitude: 2.5 cm. Species: A. araucana, N. antarctica, P. contorta, P. sylvestris. Conditions: A araucaria, API araucaria-pine, NI ñirre, ÑIPI ñirre-pine, PI pine

condition had more biomass than ñirre and the ñirrepine condition (Fig. 4). The araucaria condition had a biomass of 77,735.7 (\pm 25,952) kg ha⁻¹ for the total crown component, which was significantly higher (F: 3.0; p < 0.05) than the other conditions. Ñirre had 25,002.6 (\pm 6,259) kg ha⁻¹ and pine 21,581.6 (±4,158.5) kg ha⁻¹, both with the lowest biomass of the total crown component (Fig. 4). The total biomass of the araucaria and araucaria-pine condition, reached values of 354,213.7 (±106,880.9) kg ha⁻¹ and 323,361.1 (±89,916.1) kg ha⁻¹, significantly higher (F: 483, p < 0.05) than the pine condition, which had



Fig. 4 Fuel load (kg ha⁻¹) by components within conditions studied. Letter a-c show significant ($\alpha = 0.05$) differences between conditions by Tukey pairwise comparison. Standard error shown in *error bars*. Conditions: A araucaria, API araucaria-pine, NI ñirre, NIPI ñirre-pine, PI pine. Components:

the lowest biomass of 67,692.8 ($\pm 10,211.9$) kg ha⁻¹ (Fig. 4). The higher biomass in the araucaria and araucaria-pine conditions in the tree layer, were due to the larger size of *A. araucana* trees (greater biomass per tree) in comparison to *P. contorta*, *P. sylvestris*, and *N. antarctica*.

The native species *A. araucana* and *N. antarctica* had a lower biomass in the invaded than the noninvaded condition for the three canopy fuel components (Table 3). The canopy fuel biomass from the two invasive pines in the native forest is lower compared with the native species. The sum of the biomass of fine crown fuel in the pine condition, for *P. contorta* and *P. sylvestris*, was higher than the biomass that *N. antarctica* provides in the invaded and non-invaded ñirre condition (Table 3).

Vertical and horizontal fuel continuity

The araucaria, araucaria-pine and ñirre conditions showed a disruption in the vertical fuel continuity (Table 4, Fig. 5). The araucaria condition had a significantly higher disruption of fuel than araucariapine (p < 0.05, Table 4). No significant differences were detected when comparing the other conditions due to little or no disruption of fuel. *Pinus contorta*



Fine d. f.: fine downed woody fuel (< 0.6 cm), Coarse d.f.: Coarse downed woody fuel (0.6–7.5 cm), Fine c.f.: fine crown fuel (foliage + branches 0–0.6 cm), Coarse c.f.: coarse crown fuel (branches 0.6–7.5 cm), Crown b.: crown biomass, Total b.: Total biomass (canopy, understory and debris)

increased the vegetation cover in the invaded ecosystems (ñirre and araucaria) enhancing the vertical and horizontal continuity of fuel (Fig. 5).

In the horizontal fuel continuity, no significant differences were found for any condition. The pine condition had the highest value of accumulative crown area and araucaria the lowest value (Table 5). The accumulative crown area in the invaded condition of araucaria showed a higher value than the non-invaded (Table 5). The crown area of *A. araucana* in the araucaria and araucaria-pine condition showed no difference. *Nothofagus antarctica* had a higher crown area and tree density in the ñirre condition than in ñirre-pine. In the ñirre-pine condition the tree density and crown area of *P. contorta* and *P. sylvestris* was similar to *N. antarctica*. The pine condition had the highest tree density and crown area, compared with the other conditions (Fig. 6).

Species differences

Fuel flammability

Araucaria araucana had the highest foliar moisture content, followed by *N. antarctica*, *P. contorta* and *C. culeou* with the lowest value. *Chusquea culeou* was

Condition	Species	Canopy fuel (kg ha ⁻¹)		
		Fine crown f.	Coarse crown f.	Tree
Araucaria	A. araucana	30,517.7 (10,427.5)	47,218 (15,539.6)	314,062.6 (110,355.8)
Araucaria-pine	A. araucana	28,018.3 (8009.6)	39,528 (12,188.8)	28,8370.3 (86,651.9)
	P. contorta	2,171.3 (567.2)	1,605.7 (517.5)	6,474.8 (1805.6)
	N. antarctica	31.5 (26.6)	35.7 (30.2)	185.4 (156.7)
	P. sylvestris	212.7 (154.8)	99.6 (79.0)	586.5 (445.7)
Ñirre	N. antarctica	7,974.3 (2,285.6)	25,583.7 (10,052.6)	59,788 (14,558.1)
Ñirre-pine	P. contorta	1,724.4 (687.3)	1,047.7 (446.5)	4,839.8 (1978.4)
	N. antarctica	7,483.5 (2,399.6)	23,816.8 (8,195.9)	59,527.8 (19,509.6)
	P. sylvestris	4,36.4 (368.9)	263.9 (223.1)	1288.7 (1,089.2)
Pine	P. contorta	9,760.4 (2,833.8)	7,838.4 (1,778.1)	29,981.9 (7,887.3)
	P. sylvestris	2,480.6 (1,421.9)	2,695.6 (1,281.8)	8,677 (4,616)

Table 3 Canopy fuel load for tree species

Mean dry weight for components (standard error), within studied conditions. Components: Fine crown f.: fine crown fuel (foliage + branches 0-0.6 cm), Coarse crown f.: coarse crown fuel (branches 0.6-7.5 cm), Tree: total tree biomass

 $\label{eq:continuity} \begin{array}{c} \textbf{Table 4} & \text{Disruption of vertical fuel continuity (m) within conditions} \end{array}$

Conditions	Mean (SE)	t value	$\Pr > t $
Araucaria Araucaria-pine	6.3 (1.3) 1.2 (1.1)	-2.95	0.0215
Ñirre Ñirre-pine	0.3 (0.2) 0.03 (0.03)	1.43	0.2238
Conditions	Mean (SE)	F value	Pr > F
Araucaria-pine Ñirre-pine Pine	1.2 (1.1) 0.03 (0.03) 0 (0)	1.1	0.3638

t T-student test, F one-way ANOVA, SE standard error

significantly different from the other species (p < 0.0001) and *A. araucana* moisture content value was different from *P. contorta* (F: 39.97; p < 0.0001). *Pinus contorta* and *C. culeou* had significantly higher volatile content (F: 154.2; p < 0.0001) than *N. antarctica* and *A. araucana*, the latter species with the lowest value (Table 6). The higher calorific value for the four species was significantly different (F: 87.87; p < 0.0001), *A. araucana* had the lowest value and *P. contorta* the highest.

For the three species there is a negative relation between the proportion of the fine fuel (foliage + branches <0.6 cm) and the DBH, contrariwise the coarse fuel (branches > 2.5 cm) increases with the DBH (Fig. 7). *Pinus contorta* and *P. sylvestris* had more proportion of fine fuel than *N. antarctica*. The latter had higher fuel of medium branches (0.6–2.5 cm) in the trees with lower DBH and when the DBH increases, the thicker branches (>2.5 cm) proportion increase as well. *Pinus sylvestris* had highest proportions of fine fuel for all DBH classes (Fig. 7).

There were significant differences (F: 9.26; p < 0.0003) in the packing ratio of the fine crown fuel (Fig. 8). *Nothofagus antarctica* had 0.095 (±0.01) kg m⁻³ of crown bulk density, a value significantly lower (F: 9.26; p < 0.0003) than *P. sylvestris* with 0.225 (±0.03) kg m⁻³ and *P.contorta* with 0.229 (±0.03) kg m⁻³ (Fig. 8).

Discussion

Ecosystem differences

The invasion of *P. contorta* has already changed the fuel properties in the Malalcahuello Reserve, modifying the forest vertical continuity and flammability. These results suggest that future wildfires would be more intense and if these changes persist or increase after several fires, the fire regime potentially could be modified. However, our findings show fewer changes in biomass and fuel accumulation probably because this is still a relatively new invasion where *P. contorta* has not reach mature conditions.



Fig. 5 Vertical vegetation structure and disruption of vertical fuel continuity. Height (m) of vegetation and cover (%) within studied conditions. Conditions: *A* araucaria, *API* araucaria-pine,

NI ñirre, NIPI ñirre-pine, PI pine. Species: Aa: A. araucana, Na: N. antarctica, Pc: P. contorta, Ps: P. sylvestris, CHc: C. culeou

Table 5 Horizontal fuel continuity

Conditions	Mean (SE)	t value	$\Pr > t $
Araucaria	3,653.2 (1,234.5)	1.3	0.2301
Araucaria-pine	5,840.2 (1,144.3)		
Ñirre	7,998.5 (2,556.6)	1.22	0.2583
Ñirre-pine	4,580 (1,164.5)		
Conditions	Mean (SE)	F value	Pr > F
Araucaria-pine	5,840.2 (1,144.3)	3.35	0.0697
Ñirre-pine	4,580 (1,164.5)		
Pine	9,899.7 (2,061.6)		
Araucaria-pine Ñirre-pine Pine	5,840.2 (1,144.3) 4,580 (1,164.5) 9,899.7 (2,061.6)	3.35	0.069

Accumulated crown area within conditions (m² ha⁻¹). t T-student test, F one-way ANOVA. SE standard error

The differences in fine downed woody fuel suggest that *N. antarctica* has more dry twigs providing greater quantity of debris than the other species. For the other fuel components evaluated in the understory and debris, a decrease tendency of biomass in the invaded condition was observed. This is consistent with Dibble and Rees (2005), who studied the effect of different invasive shrub species in fuel accumulation, concluding that the invaded condition had a lower biomass and litter depth (for the fine downed woody biomass there

was no definite trend), and only found increases in coverage, frequency, and height of shrub layer. The effect of invasive species on fuel is not fully understood and depends on the species and the native vegetation affected (Mandle et al. 2011). This was confirmed for four woody species: *Rhamnus cathartica* L. decreased the litter in the invaded area and increased the quantity of dead stems in the shrub layer (Heneghan et al. 2004; Zouhar 2011), *Robinia pseudoacacia* L. increased litter biomass in invaded areas (Stone 2009), and *Hakea sericea* Schrad. and *Acacia saligna* (Labill.) H.L.Wendl. increased the litter and fine fuel in the shrub layer and decreased herbaceous biomass in the invaded areas (van Wilgen and Richardson 1985).

The invasion of *P. contorta* had no impacts in fuel load, which is interesting because recent studies reported a negative correlation between the most invaded areas and the richness and abundance of native flora in the Malalcahuello Reserve (Urrutia et al. 2013). However, this shows that the decline in biodiversity is not represented in biomass; this could be due to the age of the pines, which are mostly young. The same effect on diversity in native flora has been reported by the invasion of *P. radiata* in Southern Marin County, California (Steers et al. 2013). This



Fig. 6 Accumulative crown area $(m^2 ha^{-1})$ and tree density (No. trees ha^{-1}) by species within the conditions studied. Trees were sorted from smallest to largest. When all the trees are of the

suggests that changes in plant composition caused by pine invasion occur faster than the impacts on ecosystem cycles as in the fire regime. same size, a *straight line* is expected, on the contrary a *curve*. The *curve* shows greater heterogeneity in the sizes of the trees

Currently, pine invasion is affecting areas with low tree cover of the araucaria and ñirre forests, which is normal in the early stages of the invasion process of

for species			
Species	Foliar moisture content (%)	Volatile material (%)	Higher calorific value (kcal kg ⁻¹)
A. araucana	73.2 (2.4) a	93.4 (0.7) c	5,359.6 (136.1) d
C. culeou	50.6 (0.8) c	130.1 (3.1) a	7,250.9 (195.1) a
N. antarctica	68.8 (1.5) ab	106.7 (0.5) b	6,257.4 (164.2) c
P. contorta	64 (1) b	136.1 (0.3) a	8,617.6 (72.7) b

Table 6 Mean value (\pm standard error) of foliar moisture content (%), volatile material (%), and higher calorific value (kcal kg⁻¹) for species

Letters a-d show significant ($\alpha = 0.05$) differences between species by Tukey pairwise comparison



Fig. 7 Fuel size arrangement (%) of P. contorta, P. sylvestris, and N. antarctica by DBH category

pioneer species with high capacity for regeneration (Kral 1993; Klinka 2002). The process of infilling in relatively more open natural forests, was confirmed by the fact that the fuel accumulation of A. araucana and N. antarctica was lower in the invaded condition than in the non-invaded forest. This would explain why in most fuel components the biomass was lower in the invaded condition, due to the young age of P. contorta trees and the high variability in the size and density found in the actual populations. Considering that the invasion was in an early stage and homogenization of the invaded stands has not been achieved, the potential growth of the trees is still high, suggesting that the canopy fuel load will increase over time. The same occurred when evaluating the fuel horizontal continuity, where the accumulative crown area provided by P. contorta was not significantly higher in the invaded areas, due to the heterogeneity found in the sample plots. When tree growth and the area occupied reach a plateau, we expect that the crown area will get to similar values as in the pine condition, and will result in higher horizontal fuel continuity in the invaded forests.



Fig. 8 Crown bulk density (kg m⁻³) for *N. antarctica*, *P. contorta*, and *P. sylvestris*. Letter a-b show significant ($\alpha = 0.05$) differences between species by Tukey pairwise comparison. Standard error showed in *error bars*

The fuel vertical continuity was the only factor, in terms of fuel structure at the ecosystem level, where the invasion of *P. contorta* had a measurable impact. The araucaria-pine condition showed a significant decrease in the disruption of vertical vegetation. This decrease will facilitate the vegetation to act as ladder

fuel causing crown fires, which are more intense and cause more damage (Scott and Reinhardt 2002). In the araucaria-pine condition, as the DBH and height of P. contorta increase, the discontinuity will be less and in the ñirre-pine condition the height of P. contorta will surpass the height of N. antarctica, which will cause a light competition between the two species and could affect N. antarctica regeneration. According to Veblen et al. (1996), the establishment of seedlings of Nothofagus spp. is best under moderately light conditions. Several studies agreed that the establishment of N. antarctica increases with decreasing tree cover (Tejera et al. 2005; Bahamonde et al. 2011, 2013). Changes in the vertical structure have been reported in South Africa in the fynbos scrub ecosystem invaded by woody species H. sericea and A. saligna (van Wilgen and Richardson 1985).

Species differences

The most flammable species are *P. contorta* and *C.* culeou, with the lowest foliar moisture content. This is critical for the fire behaviour and ignitability, because the moisture content is one of the characteristics of greater influence in the combustion efficiency, and the flammability, retarding the ignition and/or reducing the probability of ignition (Montgomery and Cheo 1969; Chandler et al. 1991; Tolhurst and Cheney 1999). Pinus contorta and C. culeou had the highest volatile content and calorific value. In addition, P. contorta had more proportion of fine fuel, characteristics related to the combustibility and consumability during a wildfire. The combustibility is directly related with the energy released by burning the fuel. This energy depends of the chemical composition of the plant. The chemical composition of the species varies depending on the age, part of the plant, and the physiological state or growth. In living plants, cellulose constitutes 75 %, meanwhile lignin is 15-35 % of the dry weight. Thus, cellulose combustion releases less heat than lignin. In dead fuel, this proportion is inverted (Chandler et al. 1991).

There are also important variations in the moisture content of the plant, where it depends on weather conditions, mainly for the dead fuel. Living fuel plants also experience humidity variations along the year, due to age, and growth stage (Pyne et al. 1996). The results suggest that in a wildfire *C. culeou* would favour the rapid ignition and an efficient combustion.

Considering that *C. culeou* is an important element in the understory due to its high density and cover, the propagation of surface fires would be facilitated by this fuel. Also this species has a synchronized flowering, fruiting and death cycle that occurs in several decades, events that generates dry biomass more susceptible to burn (Muñoz et al. 2012).

Pinus contorta would favour crown wildfires with a slow sustainability of fire and great heat release, due to its characteristics of high flammability and high packing ratio of fine fuel in the canopy. Additionally, pines have high quantities of volatile oils, which are highly flammable. Volatile oils (terpenes) in the pine needles make up to 2 % of plant tissue and have a caloric value of 32.36 MJ kg^{-1} , twice the value for cellulose and hemicelluloses (Feng-jun et al. 2011). Ormeño et al. (2009) concluded that the concentration of monoterpenes in litter were positively correlated to the flame height and negatively correlated to residence time of the flame and the ignition delay. The contribution of volatile oils in wildfires is little, participating in the initial stages of a fire (when the moisture of fuel is lost), but it has been observed that species with high contents of volatile oils are susceptible to high intensity fires (Feng-jun et al. 2011). When comparing the studied species, N. antarctica had medium values of flammability, with a moderate caloric, foliar moisture, and volatile content, and a low proportion of fine fuel and crown bulk density. Araucaria araucana had less flammability, with low ignitability and combustibility.

Potential impacts in fire regime

Invasive plants that cause changes in the fire regimes (e.g. frequency, intensity, extension, type, and timing of fires) have the potential to modify community and ecosystem processes (D'Antonio and Vitousek 1992; Brooks et al. 2004; D'Antonio and Chambers 2006; Mandle et al. 2011). The effects of invasive species at the ecosystem level, which can cause changes in the fire regime, are increases in fuel load and changes in vertical and horizontal fuel continuity. In the long term, modifications to these components will cause changes in the fire regime; especially if the introduced species has a different chemical composition and physiognomy of the plant that can cause changes in the magnitude of wildfires through changes in fuel flammability. Our results suggests that given the

current condition of *P. contorta* invasion in the Malalcahuello Reserve, the intensity of the fires will be modified, due to increased canopy density that will decrease the speed of ignition. In addition to a low moisture content, a high volatile content, and a high caloric value of *P. contorta*, the species will cause wildfires to be more intense in the invaded araucaria and ñirre forests.

As a result of the increase of vertical fuel continuity in the invaded araucaria forest, the type of wildfires will change from a surface fire regime, prevailing in pure relatively open *A. araucana* forests (Burns 1993; González et al. 2005), to crown fires that reduce the frequency but increase the intensity of wildfires (van Wilgen and Richardson 1985; Brooks et al. 2004; Mandle et al. 2011). Ñirre forests that commonly experience crown fires, will not manifest changes in the type of fires, however the fires will be of more intensity. Summarizing, in the invaded area in the Malalcahuello Reserve, fires will be transformed from mixed fires to crown stand-replacing fires, which are more devastating, hindering the regeneration of native plants and favouring the post-fire pine recruitment.

The pine invasion in the Malalcahuello Reserve is an on-going process. Thus, the maximum density of the invasion has not been achieved (Peña et al. 2008; Urrutia et al. 2013). It is likely that when the density and size of trees increase, the biomass in the understory will decrease, as a result of less light available, and will increase the biomass of litter of pine needles (Langdon et al. 2010). In rare cases, woody invasive species can suppress fires when the invasive species are less flammable than the native species (e.g. H. sericea and A. saligna). However, under extreme climatic conditions as droughts, due to higher flammability, the frequency of high intensity fires could increase (van Wilgen and Richardson 1985). This implies that the effects of invasive woody species not only depend on the characteristics of the species, but also on weather conditions and stochastic environmental events (van Wilgen and Richardson 1985; Mandle et al. 2011). According to our results, P. contorta is more flammable, summers in Araucaria forests are dry, and considering that the invasion process is increasing the horizontal fuel continuity, and fuel load; wildfires should be more intense, extensive and severe (Mandle et al. 2011).

Many studies highlight the importance of fire as a factor that enhances the expansion of *Pinus* spp.

populations in open areas in their natural range, and in invaded areas (Richardson 1998; Harvey et al. 2011; Núñez and Raffaele 2007; Zalba et al. 2008). This capacity of pine expansion reflects the high invasiveness of *P. contorta* and the rapid colonization of new areas in absence or after fire events (e.g. Despain 2001; Ledgard 2001; Johnstone and Chapin 2003; Peña et al. 2008; Langdon et al. 2010).

The intensity of the fire events can influence the regeneration of plants through post-disturbance environmental modifications, especially by mortality of plants and propagules (Halpern and Franklin 1990). In our study system, more intense wildfires could affect the establishment and repopulation of N. antarctica and A. araucana, the first one by diminishing their capacity to resprout, and for A. araucana decreasing the number of adult and young trees resisting the fires. It has been studied, that A. araucana recovery after fires relies first on the resistance of remnant trees and the root sprouting of young individuals and then increases density through seedling recruitments (Burns 1993; González et al. 2005, 2006, 2010a). On the contrary, N. antarctica mortality is high after wildfires, and their populations only recover by resprouting (Burns 1993).

Information regarding the effect of invasive woody species in fire regimes is slowly increasing globally but requires local long-term efforts to fully understand these processes (Mandle et al. 2011). In the Malalcahuello area, the P. contorta invasion is under progression already causing changes in plant composition, functional groups diversity (Urrutia et al. 2013), and some, but not all, fuel properties. These changes could extend into the landscape and the effects intensify as the species continues its invasive process. These impacts are important not only due to the loss of diversity, but also to the effect on the colonization processes after fire. This process would limit the establishment of native species, reducing the resilience of the ecosystems, and causing possible changes in successional trajectories, as reported for shrubs in the Patagonia of Argentina (Núñez and Raffaele 2007).

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