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Natural and anthropogenic influences on coarse woody debris stocks in *Nothofagus–Araucaria* forests of northern Patagonia, Argentina

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Abstract Coarse woody debris (CWD) is an important element driving ecological processes, strengthening ecosystem resilience and for biodiversity within forest ecosystems. However, the abundance and distribution of CWD and their relation to natural and human factors are poorly known in southern South America. In this work we studied the density and volume of CWD types in *Nothofagus–Araucaria* stands in northern Patagonia (Neuquén – Argentina) and relationships with forest composition and structure. We also studied their relationships with fire history, topography and human-related variables. Twenty-three stands with *Nothofagus pumilio*, *Nothofagus antarctica* and/or *Araucaria araucana* were sampled to estimate quantities of logs, snags and dead branches using the planar-intersect method. CWD density and volume in these forests were moderate and varied across the landscape with a spatial pattern determined by biotic, abiotic and human use–related variables. Mean CWD volume was 52.9 m^3 ha^{-1} (range: 1.6–143.7) and significantly varied among forest types and watersheds. CWD was positively related to dbh, tree height and slope, but negatively related to tree density. CWD was clearly influenced by composition and structural characteristics of stands, where the tree species traits had an important role. As well, the observed amount and type of CWD, whereby most of the stands showed low levels of old (pre-disturbance) logs/snags and poor new inputs of deadwood, may be explained by fire frequency. Firewood gathering and livestock grazing negatively affected deadwood stocks and topography counteracts this effect by limiting human access. Fire disturbance history, windthrow and dieback pulses produced by insect outbreaks and human access seemed to be the main causes that best explained CWD spatial distribution and abundance patterns in north-western Patagonian forests.

Key words: coarse woody debris, fire history, human access, stand development.

INTRODUCTION

Coarse woody debris (CWD), standing or fallen dead trees and their pieces, is an important component of forest ecosystems governing ecological processes and biodiversity conservation (Harmon *et al.* 1986). CWD has a key role in processes such as nutrient cycling (Laiho & Prescott 2004), energy flow and carbon storage (Harmon *et al.* 1990; Freedman *et al.* 1996), forest fire dynamics (Kitzberger *et al.* 1997; Hély *et al.* 2000) and tree regeneration (Veblen *et al.* 1996; Christie & Armesto 2003). In addition, some animals, including threatened species, are dependent on CWD during some part of their life cycles (Berg *et al.* 1994; Angelstam *et al.* 2003; Castro & Wise 2010).

The spatial distribution and abundance (density and volume) of CWD vary greatly among forest types depending on forest structure, composition and stand age (Harmon *et al.* 1986, 1990; Hély *et al.* 2000; Schlegel & Donoso 2008). Ecological factors like climate, disturbances such as fire or windthrow, and stand development modify the rates of input to and export from the deadwood pool, and the residence time of CWD biomass (Frangi *et al.* 1997; Hély *et al.* 2000; Rouvinen & Kuuluvainen 2001). Usually stand initiation and the transition from the understory re-initiation to the old-growth stages have higher biomass because of old (pre-disturbance) and new CWD accumulations, respectively (Harmon *et al.* 1986; Hély *et al.* 2000). Traits of tree species, such as maximum tree height and diameter or stem density and rate of decay, also might influence deadwood stocks among forests (Richardson *et al.* 2009). Human activities that directly affect the aboveground green or deadwood biomass in the forest, such as timber harvesting or firewood extraction, could alter CWD distribution and density at local and regional scales (Duvall & Grigal 1999; Fridman & Walheim 2000; Carmona *et al.* 2002; Rouvinen *et al.* 2002;

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Christensen *et al.* 2005). The intensity of deadwood extraction for firewood may be influenced by the accessibility of the forest and the degree of human selectivity among firewood species (Carmona *et al.* 2002). Forest use could be restricted by topography, access (e.g. presence of trails/tracks or legal restrictions) or distance from settlements to the forest (Christensen *et al.* 2005).

Despite the importance of CWD for ecological processes and habitat requirement for endangered species and management, there is a lack of published quantitative data on distribution and abundance of deadwood in temperate forests of southern South America. The few existing studies are of old-growth evergreen temperate rainforest in Chile (Carmona *et al.* 2002; Schlegel & Donoso 2008). In the rest of the southern hemisphere, data about CWD quantities and their variation among forest types have been recently published (Woldendorp & Keenan 2005; Roxburgh *et al.* 2006; Richardson *et al.* 2009).

The natural dynamics of temperate forests in southern Chile and Argentina that drive CWD stock variation is mainly associated with volcanic eruptions, fire, windthrow, insect outbreaks and extensive dieback disturbances influenced by climatic variability (Veblen *et al.* 1992, 1996, 1999; Suarez *et al.* 2004; Swanson *et al.* 2013). On the other hand, firewood extraction is common in northern Patagonia, especially in areas where indigenous people (Mapuche) use firewood for winter heating (Aagesen 2004). As a result, the actual distribution and abundance of CWD might be determined by natural and anthropogenic fires and by firewood use history. The impacts of these disturbances on CWD might be different among forest types if tree species differ in their responses to these factors, especially if the evolved angiosperm and conifer species have different rates of decay and human selection for firewood.

The main goals of this study were (i) to estimate and compare the abundance (density and volume) and type (logs, snags, branches) of CWD in pure and mixed *Nothofagus–Araucaria* forests in northern Patagonia, Argentina; (ii) to characterize the quantities of CWD in stands with different fire and firewood extraction histories and (iii) to evaluate the effect of topography, distance to trails and route-tracks on CWD attributes at stand and site level.

This work is a contribution to the understanding of the effects of natural and human disturbances, and their relationship with biotic and abiotic factors, on the characteristics of CWD in temperate forests of northern Patagonia. Our data have direct implications for future studies on fire ecology (fuel variation according to forest succession and human land use) and for habitat evaluation for endangered species that depend on CWD. Scientists expect significant changes in composition, structure and biogeography of forests due to tree mortality produced by stronger and persistent droughts and by extensive wildfires induced by global warming (Allen *et al.* 2010; Holz *et al.* 2012). In this context, our data could be used as a baseline of information to increase the understanding of the effects of climate change on the characteristics of CWD stocks in the future scenario.

METHODS

Study area

The study was conducted in Rucachoroy basin (39°14′06.3″S – 71°10′41.3″W) inside and outside Lanín National Park (Neuquén Province – Argentina) in an area covering 60 km^2. This region in the Andean cordillera is characterized by lakes, valleys and mountains within an altitude range between 1150 and 2000 m asl. Within the study area, rainfall varies between 1500 and 1800 mm annually and decreases sharply from west to east. Precipitation occurs mainly during the colder period of the year (April to September), with summer (December to February) often being very dry. Much of the winter precipitation falls as snow. Average January air temperatures are 17–19°C and average July temperatures are 7–8°C (De Fina 1972).

The vegetation at the study site is characterized by *Araucaria araucana* and *Nothofagus* spp. forests forming different associations according to altitude, exposure and soil. *Araucaria araucana* forms mixed forests with *Nothofagus pumilio* at high altitudes, above 1200 m to the upper forest limit, and with the tall shrub *N. antarctica* in the valleys and in the lower portions of drier north-facing slopes. *Araucaria* also forms pure stands on poor volcanic soils and rocky slopes from 1000 to 1800 m asl. and at the eastern edge of its range. *Nothofagus pumilio* forms pure stands in deep soils mainly on south-facing slopes and pure *N. antarctica* stands are found in the bottom of valleys (Veblen *et al.* 1992).

Stand selection and sample design

We randomly selected 23 stands from six pure and mixed *Araucaria–Nothofagus* forests by a stratified sample design (Table 1). Using a vegetation map (1:30.000 scale), sampling units were established randomly according to forest type, fire regime history and firewood extraction knowledge at six sites (sub-watersheds) (Burns 1991; Rechene 2000). Stands heavily used by humans and lacking CWD were excluded from the study because they lacked natural conditions, and forests with a slope more than 30° were excluded because of the difficulty of access. Sampling units, 1–8 per stand at least 200 m apart, were established in proportion to stand size for a total of 52 units. Due to the mean size of stands (56 hectare; range: 6–254), the separation between sampling units and the spatial variability in CWD data (Waddell 2002), each sampling unit was considered an independent replicate.

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Table 1. Distribution of stands between sites, forest types, structural classes and human use levels

Site	Stand	Forest type	Fire history	Structural class	Mean slope °	Aspect	Human use
A	A1	Np	Old-fire	MT-LT	25	SE	Low
	A2	Na	Mid-fire	ST	19	SE	Low
B	B1	Aa	Old-fire	ST-LT	8	E	High
	B2	Na	Mid-fire	ST	10	E	Medium
	B3	Np/Aa	Mid-fire	ST	13	S	Medium
	B4	Aa/Na	Mid-fire	ST	9	E	High
	B5	Aa/Na	Mid-fire	ST-LT	9	E	High
C	C1	Aa	Old-fire	IR	6	SE	High
	C2	Aa/Np	Old-fire	IR	20	SW	Medium
	C3	Np/Aa	Old-fire	IR	22	SW	Medium
D	D1	Np	Mid-fire	IR	19	S	Low
	D2	Na	Mid-fire	ST	8	E	Low
	D3	Aa/Np	Mid-fire	IR	14	SE	Low
	D4	Aa/Np	Mid-fire	IR	21	SE	Low
	D5	Np/Aa	Mid-fire	IR	7	E	Low
E	E1	Aa/Np	Old-fire	IR	21	NW	Medium
	E2	Np	Mid-fire	ST-MT	16	NW	Medium
	E3	Np	Mid-fire	nd	12	N	Medium
	E4	Aa/Np	Mid-fire	IR	26	W	Medium
	E5	Np/Aa	Old-fire	ST-LT	24	W	Medium
F	F1	Aa/Na	Mid-fire	ST-MT	2	–	Medium
	F2	Np/Aa	Mid-fire	IR	23	SE	Medium
	F3	Np	Mid-fire	IR	27	SW	Medium

IR, Irregular.

Sites (sub-watersheds) are listed along a precipitation gradient from east (low precipitation) to west (high precipitation). Forest types: Np: *Nothofagus pumilio*; Na: *Nothofagus antarctica*; Aa: *Araucaria araucana*; Np/Aa; Aa/Na; Aa/Np: mixed forests. nd: no alive tree data available for stand E3.

Coarse woody debris

Coarse woody debris was estimated using the planar-intersect method (Brown 1971), an extension of the line-intercept method (Warren & Olsen 1964). Belt-transects 300 m long × 4 m wide (five segments of 60 m long each) were used to intersect any dead standing trees (snags), woody debris on the ground (logs) with stem diameter ≥10 cm or dead tree branches with stem diameter ≥8 cm and length ≥1 m. Wood pieces were intersected using a 4-m-long bamboo stick. For each log or branch intersected, we recorded total and intersected length (m), and diameter (cm) at the midpoint to estimate CWD ground cover. We identified the species of logs and branches whenever possible. The diameter at breast height (dbh) and total height was recorded for each of the intersected snags. To estimate the volume of woody residues a cylindrical shape was assumed for each piece.

Forest structure

Forest structure of living trees of all species was recorded using the rectangular 0.12 hectare plot formed by the belt-transect established for CWD estimations. All trees with dbh ≥ 10 cm were recorded. Twenty-one stands from six forest types were sampled using 41 plots in total, where we recorded between 15 and 38 trees per plot to characterize forest structure. We estimated canopy cover with point intercept methods, height, tree density and basal area for living trees. With dbh data, we assigned each plot to a specific structural class according to the structure classification used by Schlegel and Donoso (2008) for CWD studies. This classification has seven classes based on the proportion of small (ST: ≤25 cm dbh), medium (MT: 26–50 cm) and large (LT: >50 cm) trees in the stand. Using the forest structure data and additional dendrochronology information from the region (Burns 1991; Rechene 2000; Mundo 2011), fire history was interpreted and stands, following González *et al.* (2010), were also classified as mid-development post-fire (60–120 years) or old post-fire (greater than 120 years). No recent post-fire stands (less than 60 years) were available (Table 1; Fig. 1). At the study area, fire history is regionally characterized by the existence of synchronized fire events promoted by climate variability and human use patterns (Mundo *et al.* 2013). Fire frequency in the *Araucaria* forests of Argentina was low before mid-19th century, increased since 1850 and especially during 1880–1920 associated with the Euro-Argentinean settlement and sharply decreased from the early 20th century due to the creation of Lanín National Park and the application of a fire suppression policy (Mundo *et al.* 2013). At the study site, the last fires occurred in 1934 and 1940 and affected mainly *N. antarctica* forests with or without *A. araucana*, and partially *N. pumilio*–*A. araucana* forests. Several simultaneous wildfires occurred at a regional scale in mixed *A. araucana*–*N. pumilio* forests or in pure *N. pumilio* forest between the

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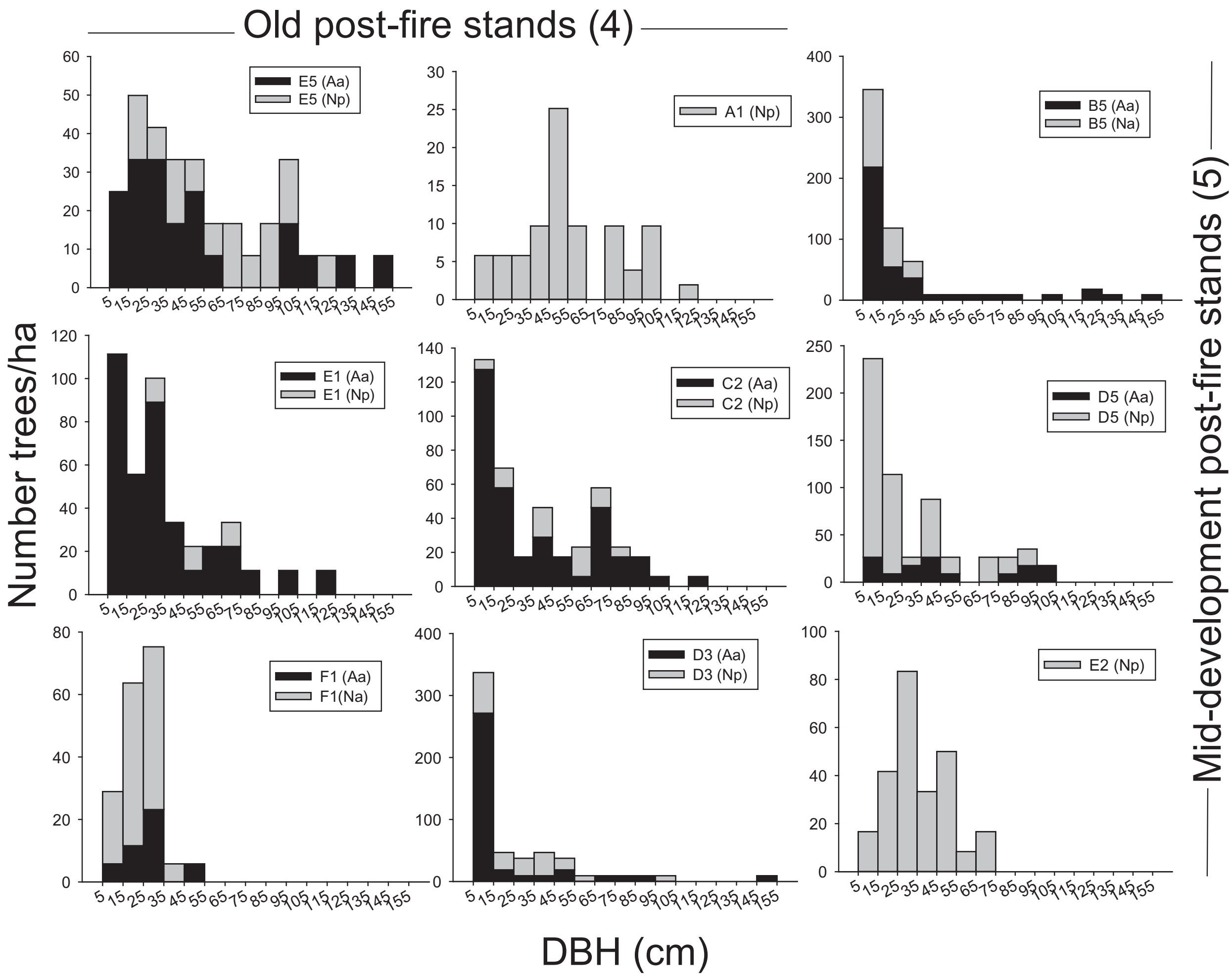

Fig. 1. Density of living trees distributed by diameter at breast height for Araucaria (Aa) and/or *Nothofagus pumilio* (Np) or *Nothofagus antarctica* (Na) representative stands (only old post-fire or mid-development post-fire classes are shown). Stands codes are shown.

years 1835 and 1907 (Mundo *et al.* 2012) producing today mid-development post-fire or old-growth-fire forest structures (Fig. 1). Irregular (IR) structures (multimodal age structures) observed on *A. araucana–N. pumilio* stands were probably generated by multiple fire events during this period. Some stands showed Old-growth structures (e.g. MT-LT) typically resulting from a long period (about 200 years or more) without fires (Fig. 1) (Burns 1991).

Topography and firewood use and explanatory variables

Current and historical firewood uses were estimated by surveys of local settlers and park rangers. During the interviews, information about levels of firewood extraction per family and per sites, preferred species, wood sizes and time since the site was used was recorded. All this information was geo-referenced using detailed vegetation and hydrology maps (1:30.000 scales) where we also previously mapped the roads, tracks, trails and settlements near the study site. Sites and stands were classified according to human use intensity, in terms of the annual wood extraction rate and considering its temporal extent. Highly used sites were those exploited by humans at least since the beginning of the 19th Century. Sites with moderate use were those used during the last 20–30 years and low use sites were those without use or only in use during the last 10 years (Table 1). To evaluate the association among firewood use, CWD stocks and forest type, we tested several potential explanatory variables: distance to settlers, distance to roads, distance to trails and number of cattle and sheep dungs as a surrogate of livestock relative abundance in forest. Also the terrain aspect and slope were used as topographic variables.

Data analyses

Mean dead wood density and volume per hectare for each woody type were calculated and used as dependent

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variables for each forest type and site to characterize the abundance and spatial distribution of woody debris in the landscape. For continuous and discrete dependent variables, we applied log (ln (variable +1)) and square-root transformations to meet normality and homoscedasticity requirements before General Linear Models were performed. We used unequal N Tukey's HSD test for comparing pairs of means among forest types, structural classes, fire history classes and CWD distribution categories.

To analyse the relationship between CWD attributes and those variables associated with forest structure, topography and human use, we used two different approaches. First we performed linear regression and correlation analysis between CWD transformed data and tree height, dbh and cover, basal area and mean stand density or with distance to settlers, to routes or to trails. Second, we explored the association between forest structure or explanatory human use variables and CWD with a Principal Component Analysis (PCA) method using the stands and forest types as objects. Before the PCA was performed, all the variables were standardized. Data from each segment for every belt-transect were standardized by subtracting its sample mean from the value of each observation and then dividing this difference by the sample standard deviation within each transect separately. Monte Carlo permutation tests were performed on the component axes selected with the PCA to investigate the statistical significance of the impact variables on axes. Stands with different firewood use (null-low *vs.* medium or high use) were grouped and the standardized mean values, within forest types, of CWD density and volume were calculated. We compared their distributions with Bootstrap tests.

RESULTS

Coarse woody debris density, volume and composition

Overall mean density (pieces per hectare) and mean CWD volume (m^3 ha^{-1}) in *Nothofagus–Araucaria* forests were 405 (± 41.7 SE; $n = 23$) and 52.9 (± 9.7 SE; $n = 23$), respectively. Both measurements varied significantly among sites (CWD density: $F_{(5,46)} = 9.59$; $P < 0.0001$; range: 163–604 pieces per hectare; CWD volume: $F_{(5,46)} = 8.91$; $P < 0.0001$; range: 13.3–98.8 m^3 ha^{-1}). CWD volume also varied significantly among stands ($F_{(22,29)} = 5.07$; $P <$ 0.0001; range: 1.7–143.7 m^3 ha^{-1}), but only 4% of the total pair comparisons were statistically significant and involved 13 of the 23 stands (Table 2). The majority of CWD was fallen branches (small logs) or

Table 2. Coarse woody debris abundance and forest structure characteristics of living trees

		CWD variables		Structure living tree variables (mean values)				
Stand	Forest type	Pieces (# ha^{-1})	Volume (m^3 ha^{-1})	dbh (cm)	Density (trees per hectare)	BA (m^2 ha^{-1})	Height (m)	Cover (%)
A1	Np	525 (104)	121.0 (28.1)	56.8	128	32.3	12.4	62
A2	Na	683 (101)	41.1 (14.4)	21.8	622	22.6	5.9	57
B1	Aa	79 (63)	1.6 (1.0)	33.9	139	13.6	8.3	35
B2	Na	212 (37)	14.2 (9.7)	17.1	720	24.5	5.4	61
B3	Np/Aa	200 (0)	14.1 (0)	16.9	489	11.0	5.8	52
B4	Aa/Na	167 (38)	29.2 (11.7)	27.8	449	25.5	6.7	37
B5	Aa/Na	158 (42)	7.3 (2.2)	34.4	374	35.0	8.0	54
C1	Aa	235 (50)	22.1 (7.8)	42.9	630	91.6	9.3	68
C2	Aa/Np	454 (13)	71.0 (27.9)	43.7	322	49.6	11.5	72
C3	Np/Aa	521 (71)	26.6 (10.5)	38.1	366	41.7	9.8	73
D1	Np	475 (0)	45.5 (0)	36.2	242	24.9	8.8	69
D2	Na	20 (29)	6.9 (3.6)	22.7	971	37.1	–	68
D3	Aa/Np	325 (221)	113.0 (40.7)	37.6	322	33.3	9.4	81
D4	Aa/Np	687 (104)	71.4 (1.3)	34.3	321	30.1	9.8	54
D5	Np/Aa	475 (50)	49.9 (14.4)	36.0	458	44.7	7.8	89
E1	Np	608 (0)	36.7 (0)	37.1	378	40.9	8.5	67
E2	Np	475 (0)	92.0 (0)	35.3	250	24.5	12.9	62
E3	Aa/Np	342 (0)	113.0 (0)	nd	nd	nd	nd	nd
E4	Aa/Np	825 (0)	143.7 (0)	38.7	404	47.5	10.0	74
E5	Aa/Np	400 (0)	143.0 (0)	58.8	283	76.1	11.1	61
F1	Aa/Na	150 (0)	4.8 (0)	23.5	432	18.2	5.7	35
F2	Np/Aa	546 (162)	37.0 (9.7)	31.3	630	32.1	6.9	87
F3	Np	487 (62)	46.6 (0.1)	48.4	175	29.3	11.8	67
Mean		405 (41)	52.9 (9.7)	35.3 (2.4)	425.2 (43.9)	37.2 (4.3)	9.0 (0.5)	63.0 (3.1)

BA, basal area; CWD, Coarse woody debris; dbh, diameter at breast height.

CWD abundance and volume are shown together with density, basal area, maximum height and cover of living trees (dbh ≥ 10 cm) for each sampled stand. Mean values (± SE) are shown. nd: no alive tree data available for stand E3.

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Table 3. Significance of differences in CWD characteristics for the different forest types and structural classes

Tukey's	Np	Aa	Na	Np/Aa	Aa/Np	Aa/Na
Np		**0.001**	**0.001**	0.339	0.999	0.053
Aa	**0.044**		0.999	0.229	**0.001**	0.903
Na	0.735	0.522		0.359	**<0.001**	0.968
Np/Aa	0.999	0.061	0.851		0.320	0.894
Aa/Np	0.999	**0.017**	0.376	0.996		**0.049**
Aa/Na	0.130	0.999	0.754	0.167	0.063	

Tukey's	ST	ST-MT	ST-LT	IR	MT-LT
ST		0.062	0.963	0.366	0.067
ST-MT	**0.007**		0.088	0.844	0.932
ST-LT	0.997	**0.047**		0.052	**0.014**
IR	**0.031**	0.966	0.118		0.597
MT-LT	0.083	0.999	**0.041**	0.988	

CWD, Coarse woody debris; IR, Irregular

Unequal N Tukey's HSD post-hoc ANOVA results for CWD density (lower-left half) and volume (Top-right half) data comparison against forest types (Above) and structural classes (Below). Bold type represents *P* values lower than 0.05. Np: *Nothofagus pumilio*; Aa: *Araucaria araucana*; Na: *Nothofagus antarctica* pure forests; Np/Aa, Aa/Np and Aa/Na are mixed forest dominated by the first cited species.

dead branches on alive trees, which were 49 and 24% of total CWD, respectively. However, logs and snags represented 40% (19 m^3 ha^{-1}) and 36% (17 m^3 ha^{-1}) of the total volume of CWD. Mean density (± SE) of *N. pumilio*, *N. antarctica* and *A. araucana* species logs was 92 (14), 30 (7) and 6 (2), respectively; whereas density for snags was 20 (5), 49 (10) and 15 (9), respectively.

Coarse woody debris characteristics for the different forest types

Density and volume of CWD varied significantly among forest types ($F_{(5,46)} = 4.56$; $P < 0.01$ and $F_{(5,46)} = 9.83$; $P < 0.0001$, respectively; Table 3). *Araucaria araucana–N. pumilio* mixed forests had more than twofold higher density of CWD than pure *A. araucana* and threefold more than mixed *A. araucana–N. antarctica* forests. CWD was three times as abundant in *N. pumilio* mixed forests as it was in *A. araucana–N. antarctica* forest. *Nothofagus pumilio* and *A. araucana–N. pumilio* forests had more than fourfold CWD volume than pure and mixed *A. araucana–N. antarctica* stands. Variability in fallen branches ($F_{(5,77)} = 5.38$; $P < 0.001$), snags ($F_{(5,78)} = 3.03$; $P = 0.01$) and logs ($F_{(5,77)} = 3.05$; $P = 0.01$) all contributed to differences in CWD volume among forest types. *Nothofagus pumilio* forest had a greater volume of fallen branches than *A. araucana–N. antarctica* ($P < 0.008$) or than *A. araucana* ($P < 0.01$) forests. The same was observed between *A. araucana–N. pumilio* and *A. araucana–N. antarctica* forests ($P < 0.03$). *Nothofagus pumilio* had a greater volume of snags ($P < 0.02$) than *A. araucana–N. antarctica* forests and the same was observed for volume of logs between *N. pumilio* and *N. pumilio–A. araucana* forests ($P < 0.03$). Mixed forests had a greater CWD volume than pure forests ($F_{(1,50)} = 5.11$; $P < 0.03$), but no differences were found between *Nothofagus*-dominated and *Araucaria*-dominated forests ($F_{(1,50)} = 2.72$; $P = 0.105$).

Coarse woody debris characteristics in relation to forest structure

The studied stands had medium-to-small diameter tree sizes where mean dbh varied between 17 and 59 cm and basal area (BA) between 11 and 92 m^2 ha^{-1} (Table 2). CWD volume and density varied significantly ($F_{(4,32)} = 5.12$; $P < 0.003$ and $F_{(4,32)} = 7.00$; $P < 0.001$, respectively) among forest structural classes for *N. pumilio* and/or *A. araucana* forests (Table 3). Stands with MT-LT structure class showed significantly higher CWD volume than ST and ST-LT forests (Fig. 2b, Table 3). Stands with ST-MT structure showed significantly higher CWD density than those with ST or ST-LT and the same was observed between IR and ST-LT stands (Table 3). The strongest relationship among CWD and structural variables was found between CWD volume and dbh ($r^2 = 0.44$; $P = 0.001$) (Fig. 3). Also CWD volume was significantly greater in stands with taller mean tree height ($r^2 = 0.27$; $P = 0.006$). When CWD abundance and forest structure variables were analysed within each forest type, we found a weak relationship that was only statistically significant for some of the forest types (Table 4). CWD density was negatively related to tree cover on *N. pumilio*, and to tree height in *A. araucana–N. antarctica* forests, respectively. As well, CWD density was positively related with BA and tree density in *A. araucana* forests (Table 4). On the other hand, CWD volume was positively related to tree cover, BA and stems density in *A. araucana* and was negatively related to tree height in *A. araucana–N. antarctica* forests (Table 4). As well, CWD volume was positively related to BA in *A. araucana–N. pumilio* forests (Table 4).

Coarse woody debris volume and density in relation to successional stage

Coarse woody debris volume in *A. araucana–N. pumilio* forest increased along the successional stages after fire occurred (Fig. 2b). However, no

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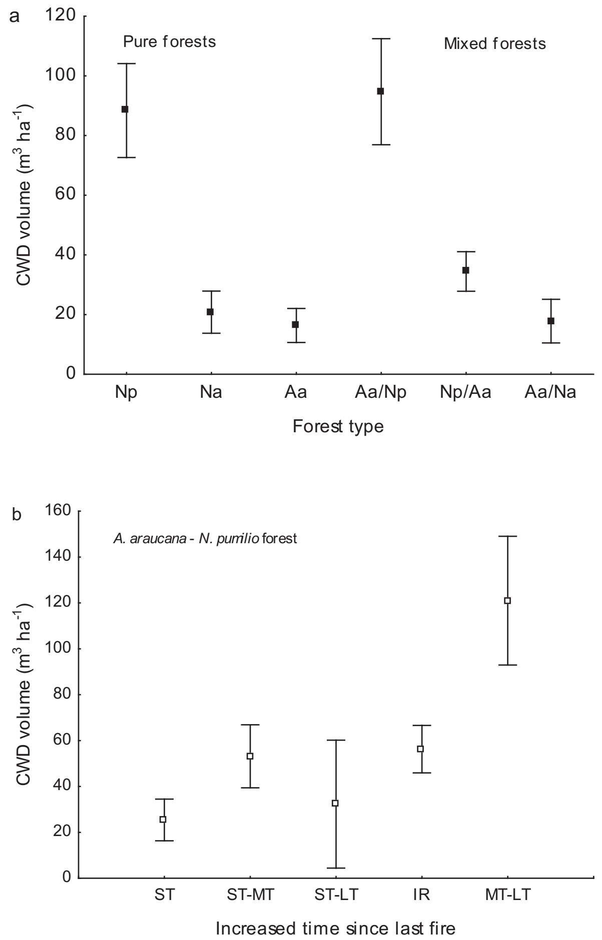

Fig. 2. Coarse woody debris (CWD) characteristics in relation to forest structure. CWD volume (m^3 ha^{-1}) variation according to stand composition and structure in pure and mixed *Araucaria-Nothofagus* sp. forest: (a) Mean volume (± SE) of different forest types; (b) Mean volume (± SE) of different structural classes. CWD: logs, snags and branches with diameter at breast height ≥8 cm and length ≥1 m. Np: *Nothofagus pumilio*; Na: *Nothofagus antarctica*; Aa: *Araucaria araucana* pure forests; Aa/Np: *A. araucana–N. pumilio*; Np/Aa: *N. pumilio–A. araucana*; Aa/Na: *A. araucana–N. antarctica* mixed forests.

significant differences on CWD volume were found between Mid-development post-fire and Old post-fire stands in any of the forest types (Np: $F_{(1,6)} = 3.44$, $P = 0.113$; Aa/Np: $F_{(1,15)} = 0.07$, $P = 0.793$; Aa or Aa/Na: $F_{(1,25)} = 0.456$, $P = 0.505$). We found similar patterns for CWD density along the successional stages and on differences among post-fire stands for any of the forest types.

Potential explanatory topographic or firewood use variables and Coarse woody debris

Actual mean firewood volume gathering per unit area and year was 1.1 m^3 ha^{-1} $year^{-1}$ and varied among sites between 0.2 and 3.0. Currently, more than 50% of the firewood is gathered from low to medium historically use level sites (e.g. D, E, B or A) because the other sites that had been used intensely in the past actually have less firewood stocks. Firewood pieces collected by settlers have between 8 and 50 cm in dbh and mostly come from logs or branches from *N. antarctica* and branches from *A. araucana*.

Coarse woody debris volumes in high and low firewood use sites were significantly lower (Monte Carlo test: $P = 0.009$) and higher ($P = 0.026$) than expectations by chance, respectively. CWD density from the three firewood use levels was all within the value ranges expected by chance.

The PCA confirmed the importance of some forest structural and human use explanatory variables for CWD abundance (Fig. 4). In general, with two and three dimensions the PCA explained, respectively, 57% and 69% of the total variance and most of the variables had a significant impact influencing on this dimensionality. The first Principal Component (PC1) showed a strong positive association (Monte Carlo test: $P < 0.01$) between CWD volume and dbh, Hmax, slope and aspect and a negative relationship with tree density and livestock abundance (Fig. 4a). On this first axis there exists an association between CWD abundance and BA, but it is not significant ($P = 0.07$). Also PC1 showed a negative association between CWD cover and the three distance variables related to human use. On the other hand, the PC2 clearly showed a significant ($P < 0.01$) and negative association between CWD cover and Tree Cover and Density (Fig. 4a). Although there is a negative association between CWD volume and distance-related human use variables, PC2 showed that this relationship is moderate ($P = 0.04$). Forest types are clearly discriminated by the positive and negative influence of the mentioned biotic and abiotic variables (Fig. 4b). *Nothofagus pumilio* and *A. araucana–N. pumilio* forests located on E, C or A sites are positively associated with those variables important for the PC1 axis and related with increasing CWD volume. On an opposite situation are those *A. araucana–N. antarctica* or *N. antarctica* forests on B and F sites where biotic and abiotic variables negatively affect CWD abundance (Fig. 4b). When the effect of forest type was excluded by the standardization of CWD data, we found that the human use–related variables have a linear and strong relationship with deadwood abundance (Fig. 5). CWD abundance significantly decreased with increasing amounts of livestock dungs (Fig. 5a) and significantly increased with increasing distances to trails (Fig. 5b) and routes (Fig. 5c), but are not related to distance to settlers ($r^2 < 0.218$).

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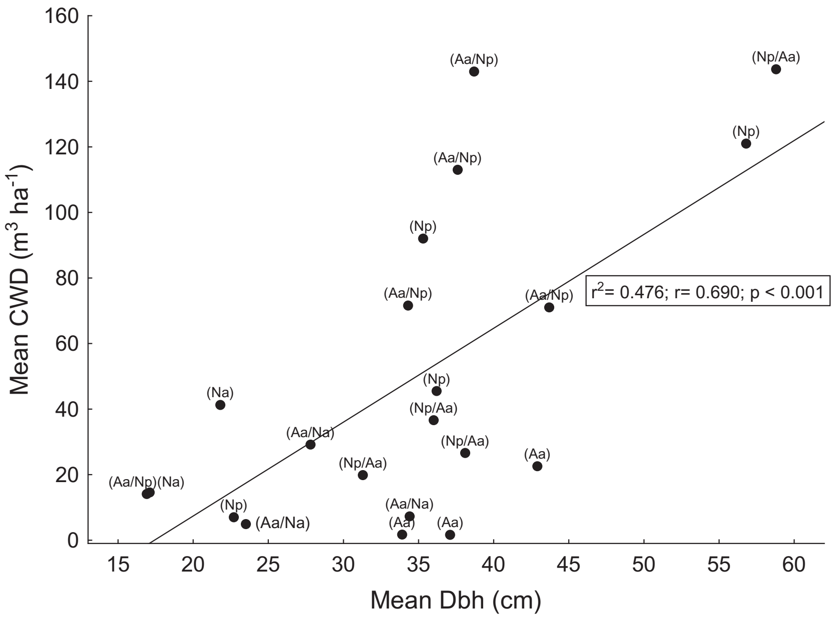

Fig. 3. Mean living tree diameter at breast height and mean coarse woody debris volume relationship at *A. araucana–Nothofagus* stands. Forest type codes are shown.

Table 4. Correlation coefficients of CWD characteristics in relation to forest structure

	Cover (%)		BA ($m^3\ ha^{-1}$)		Max height (m)		Density (tree per hectare)	
Forest	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
CWD density								
Np	**−0.86**	**0.06**	−0.34	0.58	0.34	0.58	−0.23	0.71
Na	−0.04	0.90	−0.07	0.81	0.36	0.43	−0.19	0.52
Aa	0.47	0.43	**0.69**	**0.08**	−0.28	0.65	**0.79**	**0.03**
Np-Aa	0.70	0.19	0.12	0.79	0.62	0.14	−0.46	0.30
Aa-Np	0.63	0.18	−0.39	0.30	−0.09	0.81	−0.04	0.93
Aa-Na	−0.48	0.33	−0.34	0.51	**−0.78**	**0.06**	−0.23	0.66
CWD volume								
Np	−0.62	0.18	0.05	0.93	0.73	0.16	−0.63	0.25
Na	0.07	0.82	−0.35	0.22	0.47	0.28	−0.25	0.40
Aa	**0.81**	**0.09**	**0.90**	**<0.01**	−0.38	0.52	**0.86**	**0.01**
Np-Aa	0.77	0.13	0.26	0.57	0.19	0.68	−0.07	0.89
Aa-Np	0.38	0.46	**0.67**	**0.05**	0.19	0.62	0.03	0.94
Aa-Na	−0.15	0.78	0.13	0.81	**−0.86**	**0.02**	0.54	0.27

CWD, Coarse woody debris.

Regression analysis for CWD density (pieces per hectare; square-root transformed) or CWD volume ($m^3\ ha^{-1}$; ln+1 transformed) as dependent variables and tree cover, basal area, maximum height and tree density as explanatory variables for each of the forest types. Bold highlight represents *P* values ≤ 0.10.

DISCUSSION

In this study we found moderate amounts of CWD stocks on *Nothofagus–Araucaria* forests, and their spatial distribution, type and abundance varied across the landscape influenced by a combination of biotic, abiotic and human use–related variables. The abundance of CWD is clearly influenced by the composition and structural characteristics of stands, where the tree species traits had an important role. As well, the observed abundance and type of CWD, where most of the stands showed low levels of old (pre-disturbance) logs/snags and poor new inputs of deadwood, may be explained by successional dynamics related to fire frequency and windthrow and dieback pulses produced by insect outbreaks. However, firewood gathering and livestock grazing negatively affect deadwood stocks

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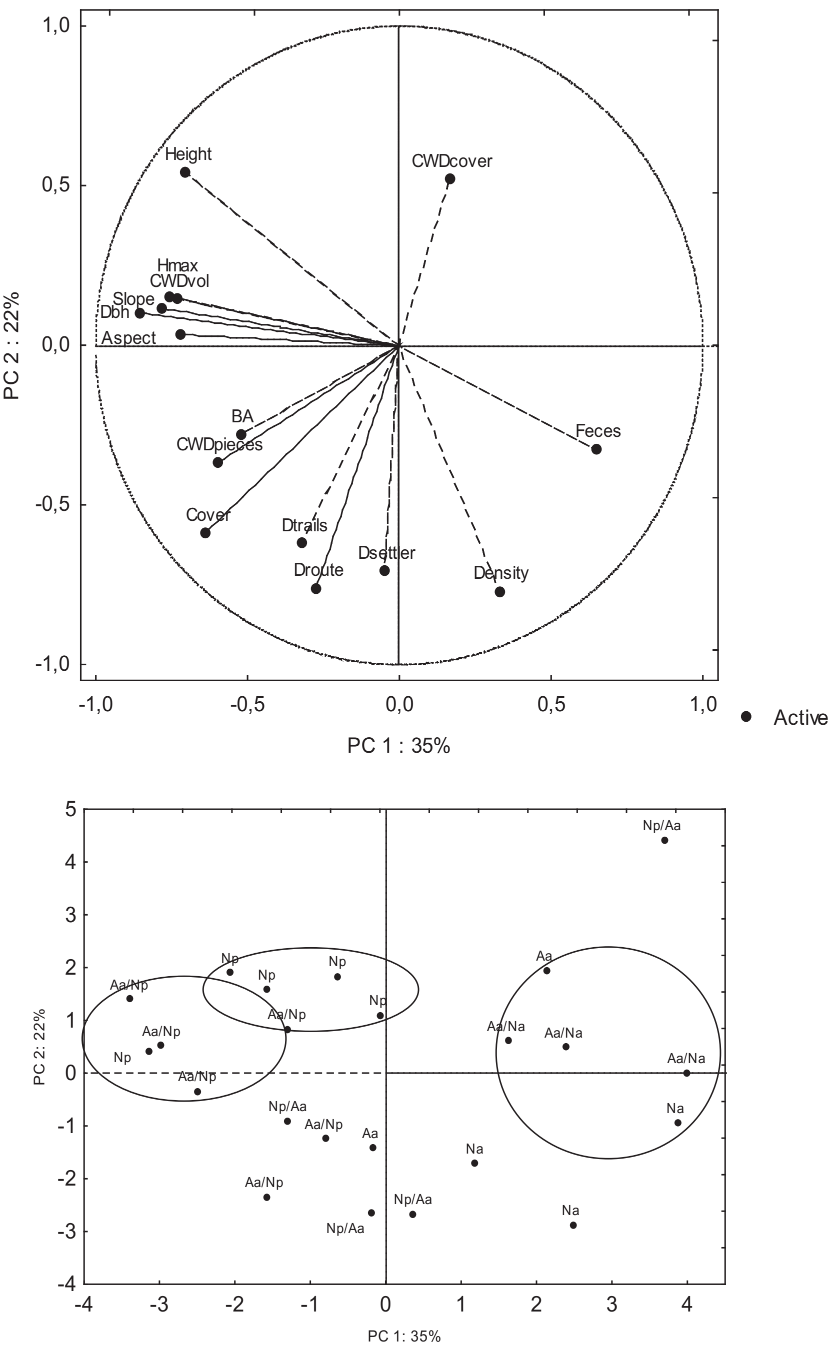

Fig. 4. Principal Component Analysis (PCA) for coarse woody debris (CWD) and explanatory variables. The PCA showing the association between CWD attributes and forest structure of living trees, topography and explanatory human use variables: (a) Variable representation for the first two principal component; (b) Representation of stands discriminated by forest type. Clustering in groups of similar forest types are highlighted with circles.

and topography counteracts this effect by limiting human access.

Coarse woody debris volume and distribution

Nothofagus–Araucaria forests in the study area are characterized by abundant small dead branches, but CWD volume is concentrated in scarce medium-size logs and snags. CWD volume estimates in this study (range: 2–144 m^3 ha^{-1}) are at the lower limit of ranges found in other temperate forests of the northern hemisphere (60–1189 m^3 ha^{-1}; Harmon *et al.* 1986). However, the mean CWD volume estimated in this study is a third to a fifth of those reported for temperate deciduous *Nothofagus* spp. forests or

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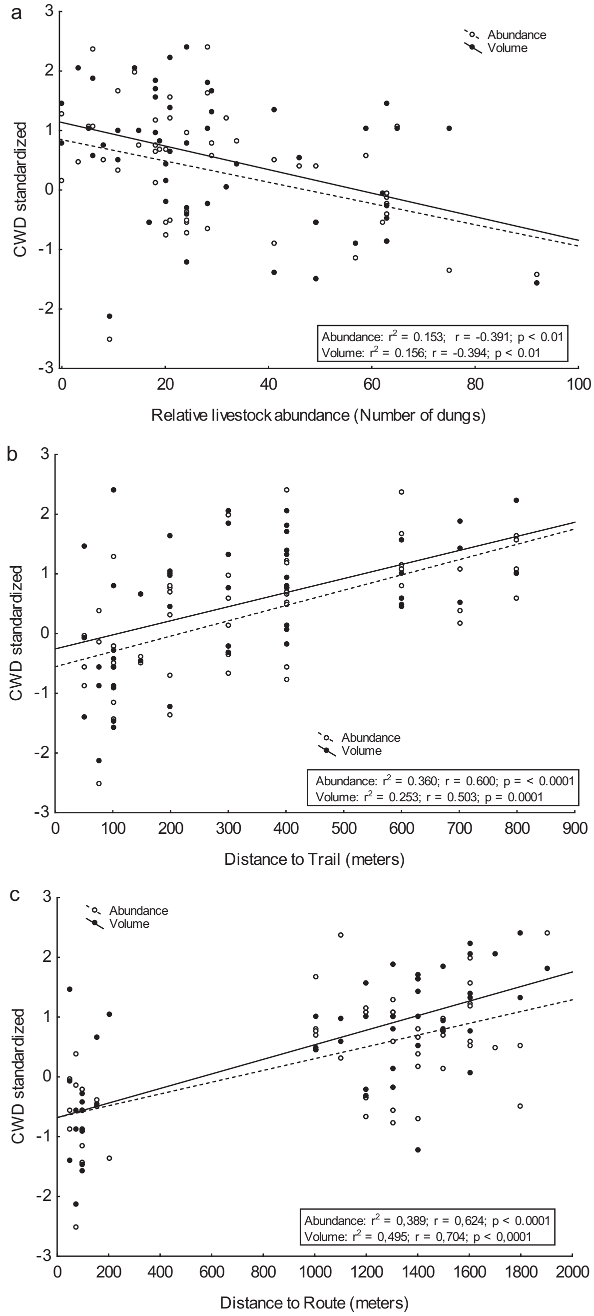

Fig. 5. Relationships between coarse woody debris (CWD) and explanatory variables. Relationship between CWD abundance and volume (standardized values), and human use potential-related variables: (a) Livestock presence (relative abundance); (b) Distance to trails and; (c) Distance to routes.

temperate rainforests in New Zealand (138 or 235 m^3 ha^{-1}; Richardson *et al.* 2009) and about a ninth of the values published for temperate rainforests in Chile (467 m^3 ha^{-1}; Carmona *et al.* 2002; Schlegel & Donoso 2008). The CWD volume found in this study is similar to that of temperate forests in Central Europe (20–60 m^3 ha^{-1}; Travaglini *et al.* 2007), but lower than that of European beech (*Fagus sylvatica*) forest reserves across the continent (130 m^3 ha^{-1}; Christensen *et al.* 2005). The reason for the lower CWD in the studied forests seems to be due to differences in stand structure rather than in composition or phylogenetic origin. As well, the fact that CWD values are similar to those of human affected European forests outside of protected areas suggests that human influence is also an important causal factor.

Coarse woody debris characteristics for the different forest types

Deadwood varied two–four folds among forest types with *N. pumilio* and mixed *A. araucana–N. pumilio* forests having the highest CWD volume; values comparable to those reported for temperate deciduous *Nothofagus spp.* forest in New Zealand (Richardson *et al.* 2009). *Nothofagus pumilio–A. araucana* had about a third of the CWD volume because of a lower density and smaller size of logs and snags. Pure and mixed stands with *A. araucana* and/or *N. antarctica* had the lowest CWD values registered in this study and were much lower than those reported by Burns (1993) for intact (not burnt or subject to human use) forests located to the north.

Tree species contribution to coarse woody debris

The tree species studied provided different density of pieces, volume and types of deadwood to the forest. *Nothofagus pumilio* provided by far the highest levels of CWD volume, ninefold and fivefold more than *N. antarctica* and *A. araucana,* respectively. *Nothofagus pumilio* CWD inputs are concentrated as logs and snags but with clear dominance of the former (density ratio log:snags 4:1), whereas *A. araucana* is concentrated as snags (ratio 1:2.5) and *N. antarctica* as snags (ratio 1:1.6). Also, *N. pumilio* provided more dead branches. This variation in CWD among the three species probably is the consequence of different life-history traits, but also may be due to human selection of firewood (see below). *Nothofagus antarctica* is the smallest and lowest longevity species, with maximum heights of 20 m, dbh of 30 cm and maximum age of 120 years. *Nothofagus pumilio* and *A. araucana* had maximum heights of 35 m and dbh up to 200 cm. However, *N. pumilio* grows faster and has a lower longevity (300- *vs.* 1000-year-old age) than *A. araucana* and this may explain the greater contribution to CWD by the former. However, *N. pumilio* CWD

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stocks depend on the succession stage of the forest (see below). *Nothofagus pumilio* CWD characteristics depended on whether the forest was pure *N. pumilio* or mixed with *A. araucana*. In pure forests, *N. pumilio* provides an abundant stock of branches and large snags and logs, whereas in the mixed forests, CWD from this species was mainly from branches, with fewer logs and snags. Forest structure and their relationship with fire history may explain these differences. In north-eastern forests, *N. pumilio* is particularly susceptible to climate variability and their relation with insect outbreaks, where both factors produce dieback pulses and tree mortality thus increasing its contribution to CWD stocks (Veblen *et al.* 1996).

Coarse woody debris density and volume and their relation with forest structure

In general, CWD density and volume were weakly related to the forest structure of living trees. Mean tree diameter was the variable most related with CWD stock, especially with volume. Direct relationships among CWD density or volume with tree cover, BA, tree density and height were especially significant in *A. araucana*-dominated forest. These results suggest that the contribution by this conifer to CWD stocks is density and tree size dependent and due to the increase in snags and branches as the trees grow and the forest becomes denser. In *N. pumilio*-dominated forest CWD volume is negatively related to tree cover or no relationship exists. These results are consistent with the greater proportion of logs in this kind of forest and its contribution to CWD stocks. The opposite pattern of logs:snags ratio in *N. pumilio* and *A. araucana* could be related to different susceptibility to fire and resistance to windthrow disturbance. Fire spreading in pure *N. pumilio* forests is lower, they often tend to serve as natural fire breaks because of higher moisture and lower summer temperature associated with southerly aspects, allowing the formation of old-growth structures where *N. pumilio* commonly fall down by windstorms and therefore producing a greater density of logs and CWD volume (Mermoz *et al.* 2005). On the other hand, *A. araucana* has several adaptations against fire (e.g. have a 20-cm-thick fire-resistant bark) and a greater ability to resist strong winds, due to their massively and extensively superficial root system (Burns 1991), therefore a snag-dominated ratio is expected. The stand structure of *N. pumilio* and *A. araucana–N. pumilio* forests indicates that they are in the re-initiation stage or approaching the old-growth stage, probably due to the absence of fire in these stands during the period of frequent wildfires (1850–1920 years) and few fires affecting them during the early 19th century (Mundo *et al.* 2013). This may explain the high quantities of deadwood and its distribution among CWD types. On the contrary, the dbh distribution of alive trees in *N. pumilio–A. araucana* forests sampled suggests that these were mainly in the stand establishment stage and therefore the density of snags and logs was lower because the intraspecific competition and mortality were negligible. The type and sizes of CWD showed that this forest type had a low quantity of old (pre-disturbance fires) and new CWD pools. This conclusion is consistent with a dendroecological study on the area, which showed that *A. araucana–N. pumilio* forests had an all-aged population with all-sized size class distribution (Burns 1991). In these forests, live and dead trees of *A. araucana* had a similar age range (100–700 and 250–700-year-old age), whereas *N. pumilio* live trees were younger (50–250 *vs.* 150–350-year-old age). The CWD in this type of forest represents a new stock after the last wildfire, which occurred probably during the period with more wildfires, or even before (Burns 1991; Mundo *et al.* 2013). The smaller sizes (10–30 cm dbh) of CWD logs and snags in *N. pumilio–A. araucana* stands suggest that these forests have a self-thinning population cohort (Burns 1991).

Potential explanatory topographic or firewood use variables and Coarse woody debris

The CWD volumes at low and high firewood use sites and the correlations between CWD and human use–related variables show that firewood extraction affects the abundance, spatial distribution and type of deadwood in the forest. The multivariate analysis clearly showed that the density of deadwood on the ground is negatively related with distance variables that indirectly measure the human pressure against the natural resource. CWD density and cover was more related to human use variables than CWD volume. Bigger pieces of CWD are more difficult to collect by humans than the smaller ones; during firewood gathering, branches and smaller logs on the ground are more often selected than snags or big logs, especially from *N. antarctica* and *A. araucana*, mostly affecting CWD density and cover. In our study site, settlers preferred these two species because according to them, they can be lit easier, have higher caloric power and last longer (Szymañski 2012). The selectivity for these two species, together with differences on life-history traits, may explain the observed opposite pattern on snag:log rates compared with *N. pumilio*. Thus, firewood extraction modifies the size distribution of CWD and this might have important implications for ecological processes like vegetation regeneration, fire dynamics and nutrient cycles, among others. CWD variability was better

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explained by distance to roads than distance to settler. The significant negative relationship between CWD abundance and livestock relative abundance shown by the PCA analysis and through the regression results suggests that the magnitude and spatial extent of this land use also affects the CWD. Livestock grazing in the area is associated with the migration to summer fields, a period when the settlers live in the forest and use firewood 6 months per year. CWD amounts are also associated with slope and aspect. The frequency and intensity of fire or windthrow disturbances are influenced by these abiotic variables, where higher and steeper or humid sites had less frequency or intensity of fire (Mermoz *et al.* 2005). Tree-fall susceptibility increased with slope and therefore CWD stocks based on logs become important. Results from the multivariate analysis suggest that the strong association between CWD volume and slope can be explained not only by the influence of ecological factors but also by the topographic constraints on human access to the forest.

Recent studies at the region demonstrated a decrease in forest growth, an increase in heat-induced tree mortality and in wildfire activity due to changes on moisture and temperature during summer (Allen *et al.* 2010; Holz *et al.* 2012; Mundo *et al.* 2012). These climate-induced trends will surely change deadwood characteristics in the future at the regional scale where we expect a decrease in CWD quantities by the conversion of extensive forest into scrublands and by a decrease in the proportion of old-growth forest structures that actually accumulate and store carbon stocks.

CONCLUSION

With this work we showed that the abundance, type and spatial distribution of CWD on the north-eastern forest in Patagonia are influenced by tree composition, stand development stage and firewood use, and ultimately is related with the history of natural disturbances and with the spatial pattern of human access to the forest.

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