

Site quality influence over understory plant diversity in old-growth and harvested *Nothofagus pumilio* forest

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Abstract

Aim of study: The effects and interactions of shelterwood forest harvesting and site qualities over understory plant species diversity and composition were compared among primary and harvested *Nothofagus pumilio* forests.

Area of study: Tierra del Fuego (Argentina), on three pure conditions (one and six year-old harvested, and primary without previous harvesting forests) and three site qualities (high, medium and low).

Material and methods: Understory richness and cover (%) were registered in five replicates of 1 hectare each per treatment. Taxonomic species were classified in categories (groups, origin and life forms). Two-way ANOVAs and multivariate analyses were conducted.

Main results: Shelterwood harvesting and site quality significantly influenced understory cover and richness, which allow the introduction of native and exotic species and increasing of dicot and monocot covers. In dicots, monocots, exotics and total groups, higher richness and covers were related to time. Meanwhile, cover reached similar high values in all site qualities on dicot, native and total groups. On the other hand, monocot and exotic richness and cover remain similar in primary and recently harvested forests, and greatly increased in old harvested forests. Mosses and ferns were among the most sensitive groups.

Research highlights: Impacts of shelterwood cut depend on site quality of the stands and time since harvesting occurs. For this, different site quality stands should received differential attention in the development of conservation strategies, as well as variations in the shelterwood implementation (as irregularity and patchiness) should be considered to better promote understory plant species conservation inside managed areas.

Key words: forest management; plant species conservation; Tierra del Fuego; years after harvesting.

Introduction

Timber forest harvesting affects ecological equilibrium and forest biodiversity (Haight, 1995), modifying the balance of original ecosystems. New environmental conditions of harvested stands modify community composition, ecological relationships among species and population dynamics, which eventually could lead to the extinction of sensitive species. Understory plant species composition and spatial distribution depend of biotic and abiotic environmental conditions (Fitter and

Hay, 1983), but few works analyze changes in understory at different forest site-quality stands (Warner and Harper, 1972; Brososke *et al.*, 2001).

South Patagonian *Nothofagus* Blume forests are some of the least disturbed eco-regions on earth (Mittermeier *et al.*, 2003), and understories are poor in vascular plant species richness compared to other temperate forests of the world (Moore, 1983). Moreover, these plants are usually widely distributed among different environments, although with different relative abundance (Lencinas *et al.*, 2008). During the last 25

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Abbreviations used: PF: primary forests; RH: recent (one year) harvested forests; OH: old (six years) harvested forests; H: high site quality; M: medium site quality; L: low site quality; SI₆₀: site index at a base age of 60 years; ANOVA: analysis of variance; NMS: non-metrical multidimensional scaling.

years, shelterwood was recommended for harvesting *Nothofagus pumilio* (Poeppig & Endl.) Krasser forests in Tierra del Fuego to obtain better timber yield and forest regeneration (Schmidt and Urzúa, 1982; Martínez Pastur *et al.*, 2000, 2011a, 2011b; Rosenfeld *et al.*, 2006). Shelterwood emulates natural forest dynamics through the opening of the canopy at large scale and leaving seed trees, using a set of cuttings to stimulate natural regeneration such as one or two preparation cuts, plus regeneration cut and overstory removal. Shelterwood cuts in *Nothofagus* forests also produce changes in microclimatic conditions at understory level (e.g., soil moisture, light and temperature) (Caldentey *et al.*, 2005, 2009) and in litter fluxes and decomposition processes in the forest floor (Caldentey *et al.*, 2001). Under timber production objectives, this harvesting system can lead to *N. pumilio* forest homogenization, producing loss of different habitats commonly observed inside primary forests (Martínez Pastur *et al.*, 2002). Specific responses to shelterwood cut could depend on the site quality of the stands, as well as to the time elapsed since harvesting occurs. Therefore, the aim of this work was to compare understory plant species diversity and composition in *N. pumilio* forests harvested through shelterwood regeneration cuts considering stands with different site quality and years since harvesting, and contrasting them against primary forests without previous harvesting.

Material and methods

Study sites

Data were obtained from *N. pumilio* pure forest stands located in San Justo Ranch in Tierra del Fuego (Argentina; 54° 06' SL, 68° 37' WL), where Los Castores Sawmill made harvesting. Climate is characterized by short, cool summers and long, snowy and frozen winters. Mean monthly air temperature varied from -0.2°C to 10.4°C (extremes from -9.6°C in July to 24.9°C in February) in primary forests, and from -1.0°C to 10.6°C (extremes from -11.3°C in July to 25.9°C in February) in harvested stands. Only three months per year did not have mean monthly temperatures under 0°C, and the growing season was less than five months (Barrera *et al.*, 2000). Soil (30 cm below forest floor) never freeze in primary forests, but soil freezing occurs in harvested stands (-0.2 to -0.6°C during June-July). Rainfall including snowfall was

382 mm yr⁻¹ below canopy of primary forests, while it reached to 639 mm yr⁻¹ in harvested stands. Annual average wind speed outside forests was 8 km h⁻¹, reaching up to 100 km h⁻¹ during storms.

In this undulating area, soils are shallow and have good drainage, developing in acidic brown forest soils over glacial depositions (Moore 1983), where rooting systems are mostly concentrated in the upper 30 cm depth. Regional vegetation is dominated by deciduous *Nothofagus* forests and grasslands, while understory comprises high non-vascular and low vascular plant diversities; this last dominated by natives but also with deliberately or accidentally introduced exotic plant species (Lencinas *et al.*, 2008a,b). Large native fauna include few native and exotic mammals (mousses, foxes, beavers, camelids) and several bird species, which freely feed in both forests and open areas. Also, domestic herbivore grazing can occasionally occur inside forests, since livestock and forest activities coexist without fences surrounding harvested stands in this area.

Three forest conditions were compared: two harvested forests, both cut by shelterwood harvesting but not completely yet regenerated, with different times since harvesting occurs (one year ago or recent harvested stands-RH, and six years ago or old harvested stands-OH), and primary forests-PF without previous harvesting. The harvested stands were cut and extracted for the same sawmill in the two times, with the same machines and stem extraction system. Also, three site qualities were analyzed for each forest condition, defined according to Martínez Pastur *et al.* (1997) through the site index at a base age of 60 years (SI₆₀): high site quality stands-H (SI₆₀ = 18.7-23.2 m) with total volumes up to 850 m³ ha⁻¹, medium site quality stands-M (SI₆₀ = 14.3-18.7 m) 700-800 m³ ha⁻¹, and low site quality stands-L (SI₆₀ = 9.8-14.3 m) with total volumes < 700 m³ ha⁻¹ (Martínez Pastur *et al.*, 1997, 2009). In *Nothofagus* forests, site quality present variations at several hectares or stand scale (Martínez Pastur *et al.*, 1997). These forests were undisturbed by forestry practices (pre-treatments) before silvicultural regeneration systems were in place, and retained overstory was not still harvested in none of them.

Understory measurements

Five plots of 1 hectare were selected for each situation (3 forest conditions × 3 site qualities × 5 replicas),

where understory plant species richness of each site and cover (%) were registered by relevé methodology (Kent and Coker, 1992). All vascular plants (Dicotyledoneae, Monocotyledoneae and Pteridophyta) were determined to species level, meanwhile non-vascular plants were considered as a unique group (mosses and liverworts). Taxonomy of the species follows the classification proposed by Moore (1983). Also with vegetation, bare soil cover (soil or litter on the forest floor without vegetation), and debris cover (more than 3 cm diameter branches and dead wood) were estimated. For further analyses, understory plants were grouped in different categories: (i) groups (dicots, monocots, ferns or mosses), (ii) origin (native or exotic), and (iii) life form (prostrate herbs, erect herbs, shrubs, trees, rhizomatous grasses and caespitose grasses), following Moore (1983) and Correa (1969-1998). Likewise, species were considered “exclusives” when only were found in some forest condition (PF, RH, OH) or site quality (H, M, L). Species names of vascular plants follow Moore (1983).

Statistical analysis

Two-way ANOVAs were performed to analyze the influence and the interaction of forest condition (with three levels: RH, OH and PF) and site quality (with also three levels: H, M and L) over forest floor covers and plant species richness, classified in different categories (by groups and origin). Means were separated by Tukey multiple range test at $p < 0.05$ for all the analyses. Statgraphics (Statistical Graphics Corp., USA) software was used for these analyses.

Species cover matrixes were used for multivariate analyses. Cluster analysis with correlation distance and linkage by Ward’s method was used to evaluate groups among forest condition and site quality of the stands. Multi-response permutation procedure-MRPP, also with correlation distance, was utilized to analyze cluster group significance. Multivariate ordination analyses (non-metrical multidimensional scaling-NMDS and reciprocal averaging) classified plots by site quality and forest condition, and understory plant species by origin and life form, respectively. For NMDS, Bray-Curtis distances and 9999 unrestricted random permutations of the raw data were used, and again MRPP was employed to evaluate grouping significance, with Bray-Curtis distance. PC-Ord (McCune and Mefford, 1999) software was used for these analyses.

Results

Understory characterization

There were observed 53 species of vascular plants in the whole study (33 dicots, 18 monocots and two ferns) (Table 1): 26 species were found in PF, 32 in RH and 50 in OH. Among total vegetation, 21 species were common to all forest conditions, nine were found only in harvested stands (RH and OH) but not in PF, four species were lost in RH but were present in OH and PF, and 19 species were exclusive of one forest condition: *Luzula alopecurus* was the only one exclusive (and native) species in PF, two species were exclusively observed in RH (the exotic *Capsella bursa-pastoris* and the native *Phaiophleps biflora*), and 16 species in OH (which three of them were exotics) (Table 2). On the other hand, total species richness was unequal in different site qualities, with higher total richness in M (45 species, with six species exclusively found here) than in L (40 species, with five exclusive species) and H (36 species, with only two exclusive species, Table 2). Among these, 28 species were common to all site qualities, meanwhile five were shared between M and H, six between M and L, and only one between H and L.

Exotic plant richness included 11 species in the whole study (Table 1 and 2), which four of them were shared among all forest conditions and site qualities: *Cerastium fontanum*, *Poa pratensis*, *Rumex acetosella* and *Taraxacum officinale*. The other seven exotic species arrived after harvesting, and its quantities increased over years from shelterwood: three were found in RH and six in OH. Among these exotic species, three were found in both harvested forest conditions (*Senecio vulgaris*, *Stellaria media* and *Veronica serpyllifolia*), one species (*C. bursa-pastoris*) was only found in RH, and three were exclusive of OH (*Agrostis stolonifera*, *Hieracium pilosella* and *Sagina procumbens*). Among the exotic species that only were found in harvested stands, one of them was observed in all site qualities (*S. vulgaris*), three were present in M and L (*A. stolonifera*, *S. procumbens* and *S. media*), two in M and H (*C. bursa-pastoris* and *V. serpyllifolia*), and one exclusively in H (*H. pilosella*).

Different types of forest floor cover significantly changed with forest condition and site quality (Table 3), and all cover variables except monocot cover presented interactions between these two main factors. In dicot, native and total vegetation covers, interactions emerged because similar and high values were observed in H

Table 1. Understory plant species observed in the studied *Nothofagus pumilio* forests

Code	Species	Group	Family	Origin	Life forms
ACMA	<i>Acaena magellanica</i>	Dicot	Rosaceae	N	PH
ACOV	<i>A. ovalifolia</i>	Dicot	Rosaceae	N	PH
ACPI	<i>A. pinnatifida</i>	Dicot	Rosaceae	N	EH
ADCH	<i>Adenocaulon chilense</i>	Dicot	Compositae	N	EH
AGFL	<i>Agrostis flavidula</i>	Monocot	Gramineae	N	PH
AGST	<i>A. stolonifera</i>	Monocot	Gramineae	E	RG
AGUL	<i>A. uliginosa</i>	Monocot	Gramineae	N	CG
ALMA	<i>Alopecurus magellanicus</i>	Monocot	Gramineae	N	CG
AZTR	<i>Azorella trifurcata</i>	Dicot	Apiaceae	N	S
BEBU	<i>Berberis buxifolia</i>	Dicot	Berberidaceae	N	S
BLPE	<i>Blechnum penna-marina</i>	Fern	Blechnaceae	N	EH
BRUN	<i>Bromus unioides</i>	Monocot	Gramineae	N	CG
CABU	<i>Capsella bursa-pastoris</i>	Dicot	Brassicaceae	E	EH
CAGL	<i>Cardamine glacialis</i>	Dicot	Brassicaceae	N	EH
CACU	<i>Carex curta</i>	Monocot	Cyperaceae	N	RG
CAMA	<i>C. macloviana</i>	Monocot	Cyperaceae	N	RG
CEAR	<i>Cerastium arvense</i>	Dicot	Caryophyllaceae	N	PH
CEFO	<i>C. fontanum</i>	Dicot	Caryophyllaceae	E	PH
CYFR	<i>Cystopteris fragilis</i>	Fern	Athyraceae	N	EH
DEAN	<i>Deschampsia antarctica</i>	Monocot	Gramineae	N	CG
DEFL	<i>D. flexuosa</i>	Monocot	Gramineae	N	RG
DYGL	<i>Dysopsis glechomoides</i>	Dicot	Euphorbiaceae	N	PH
ELAG	<i>Elymus agropyroides</i>	Monocot	Gramineae	N	RG
EPAU	<i>Epilobium australe</i>	Dicot	Onagraceae	N	EH
ERMY	<i>Erigeron miosotis</i>	Dicot	Compositae	N	EH
FEMA	<i>Festuca magellanica</i>	Monocot	Gramineae	N	CG
GAAN	<i>Galium antarcticum</i>	Dicot	Rubiaceae	N	PH
GAAP	<i>G. aparine</i>	Dicot	Rubiaceae	N	PH
GANI	<i>Gamochoeta nivalis</i>	Dicot	Compositae	N	EH
GEMA	<i>Geum magellanicum</i>	Dicot	Rosaceae	N	EH
HIPI	<i>Hieracium pilosela</i>	Dicot	Compositae	E	PH
HOCO	<i>Hordeum comosum</i>	Monocot	Gramineae	N	CG
LUAL	<i>Luzula alopecurus</i>	Monocot	Juncaceae	N	CG
MAGR	<i>Macrachaenium gracile</i>	Dicot	Compositae	N	RG
NOPU	<i>Nothofagus pumilio</i>	Dicot	Fagaceae	N	T
OSCH	<i>Osmorhiza chilensis</i>	Dicot	Apiaceae	N	EH
PHBI	<i>Phaiophleps biflora</i>	Monocot	Iridaceae	N	EH
PHAL	<i>Phleum alpinum</i>	Monocot	Gramineae	N	CG
POPR	<i>Poa pratensis</i>	Monocot	Gramineae	E	RG
RABI	<i>Ranunculus biternatus</i>	Dicot	Ranunculaceae	N	PH
RASE	<i>R. sericocephalus</i>	Dicot	Ranunculaceae	N	PH
RIMA	<i>Ribes magellanicum</i>	Dicot	Saxifragaceae	N	S
RUAC	<i>Rumex acetosella</i>	Dicot	Polygonaceae	E	EH
SAPR	<i>Sagina procumbens</i>	Dicot	Caryophyllaceae	E	PH
SELE	<i>Senecio leucomallus</i>	Dicot	Compositae	N	EH
SEVU	<i>S. vulgaris</i>	Dicot	Compositae	E	EH
STME	<i>Stellaria media</i>	Dicot	Caryophyllaceae	E	PH
TAGI	<i>Taraxacum gillesii</i>	Dicot	Compositae	N	EH
TAOF	<i>T. officinale</i>	Dicot	Compositae	E	EH
TRSP	<i>Trisetum spicatum</i>	Monocot	Gramineae	N	CG
UNLE	<i>Uncinia lechleriana</i>	Monocot	Cyperaceae	N	RG
VESE	<i>Veronica serpyllifolia</i>	Dicot	Scrophulariaceae	E	PH
VIMA	<i>Viola magellanica</i>	Dicot	Violaceae	N	PH

Origin: N, native; E, exotic. Life forms: T, tree; S, shrub; EH, erect herb; PH, prostrate herb; CG, caespitose grass; RG, rhizomatous grass.

Table 2. Cover percentage (mean \pm standard deviation) of understory plant species on the studied *Nothofagus pumilio* forests, considering forest condition (PF: primary forests without previous harvesting; RH, recent harvested stands, OH, old harvested stands) and site quality (H, high; M, medium; L, low). See species code in Table 1

Code	PF			RH			OH		
	H	M	L	H	M	L	H	M	L
ACMA	3.81 \pm 3.64	1.24 \pm 1.97		10.43 \pm 14.22	1.88 \pm 1.53	0.40 \pm 0.89	8.55 \pm 6.83	13.35 \pm 6.33	3.30 \pm 2.39
ACOV					0.36 \pm 0.80	0.40 \pm 0.65	0.88 \pm 1.21	4.94 \pm 4.55	
ACPI							0.16 \pm 0.22	0.32 \pm 0.29	0.10 \pm 0.22
ADCH	5.50 \pm 7.58							0.24 \pm 0.54	
AGFL	0.14 \pm 0.31		0.10 \pm 0.22	1.77 \pm 3.50		0.06 \pm 0.13	5.90 \pm 4.62	1.25 \pm 0.44	1.80 \pm 1.60
AGST								0.24 \pm 0.54	0.90 \pm 0.89
AGUL							0.40 \pm 0.89		
ALMA						0.12 \pm 0.27		0.10 \pm 0.22	0.20 \pm 0.45
AZTR								0.24 \pm 0.54	
BEBU	0.28 \pm 0.62	1.90 \pm 2.88	0.50 \pm 0.50	0.09 \pm 0.20		1.74 \pm 1.87		0.12 \pm 0.27	0.20 \pm 0.27
BLPE	7.94 \pm 4.35	0.13 \pm 0.30		0.59 \pm 0.82	0.42 \pm 0.78			2.70 \pm 3.07	
BRUN	0.05 \pm 0.11	0.20 \pm 0.45		0.85 \pm 1.90	0.06 \pm 0.13	0.60 \pm 1.34	2.85 \pm 1.35	4.75 \pm 5.18	4.60 \pm 3.51
CABU				0.34 \pm 0.76	0.14 \pm 0.19				
CACU							0.60 \pm 1.34		0.10 \pm 0.22
CAGL	0.73 \pm 1.38	3.00 \pm 1.41	3.40 \pm 2.63	9.80 \pm 11.03	17.00 \pm 9.54	42.20 \pm 15.17	0.53 \pm 0.66	1.80 \pm 4.02	1.00 \pm 1.00
CAMA								0.24 \pm 0.54	
CEAR	0.20 \pm 0.27						2.60 \pm 5.81	0.50 \pm 1.12	2.00 \pm 2.74
CEFO		1.47 \pm 1.61	1.70 \pm 1.72	3.20 \pm 6.61	37.60 \pm 7.92	1.56 \pm 1.37	11.98 \pm 13.33	7.94 \pm 4.78	26.00 \pm 6.52
CYFR	1.56 \pm 2.19	0.47 \pm 0.51		0.19 \pm 0.26	0.35 \pm 0.35	0.06 \pm 0.13	0.20 \pm 0.27	0.22 \pm 0.30	0.10 \pm 0.22
DEAN								0.36 \pm 0.80	
DEFL		0.07 \pm 0.15	0.10 \pm 0.22	0.92 \pm 0.93		0.28 \pm 0.44	0.40 \pm 0.55		
DYGL	19.07 \pm 7.30	2.07 \pm 1.92					0.16 \pm 0.36	0.22 \pm 0.30	2.10 \pm 4.42
ELAG					0.18 \pm 0.40		0.40 \pm 0.55	1.39 \pm 1.52	0.20 \pm 0.45
EPAU									0.20 \pm 0.45
ERMY								0.40 \pm 0.39	0.20 \pm 0.45
FEMA	1.00 \pm 0.97	3.64 \pm 2.73	1.80 \pm 1.30	4.03 \pm 3.96	7.06 \pm 1.97	9.60 \pm 4.04	2.38 \pm 2.06	1.48 \pm 2.23	2.60 \pm 2.19
GAAN	0.06 \pm 0.14	0.47 \pm 0.87						1.01 \pm 2.12	0.70 \pm 0.76
GAAP	3.00 \pm 0.47	1.94 \pm 2.78	2.10 \pm 2.66	11.54 \pm 14.76	13.70 \pm 7.09	13.20 \pm 4.09	3.25 \pm 0.83	6.41 \pm 4.86	11.60 \pm 7.27
GANI								0.10 \pm 0.22	
GEMA			0.10 \pm 0.22		0.09 \pm 0.20			1.01 \pm 0.80	
HIPI							0.18 \pm 0.25		
HOCO				0.17 \pm 0.38			0.33 \pm 0.47	2.68 \pm 1.91	
LUAL		0.10 \pm 0.22							
MAGR								0.24 \pm 0.54	
NOPU	14.67 \pm 1.58	38.18 \pm 22.02	24.60 \pm 12.38	10.80 \pm 5.02	7.96 \pm 5.21	13.60 \pm 2.51	38.60 \pm 13.96	16.10 \pm 7.40	10.00 \pm 6.12
OSCH	4.19 \pm 4.48	7.14 \pm 4.72	0.50 \pm 0.50	47.00 \pm 17.59	43.20 \pm 13.31	24.00 \pm 9.25	17.95 \pm 6.55	15.75 \pm 9.12	12.00 \pm 5.70
PHAL	0.90 \pm 0.94	0.90 \pm 1.24	0.60 \pm 0.55	8.70 \pm 6.80	2.58 \pm 1.55	1.50 \pm 1.00	12.30 \pm 15.09	21.10 \pm 6.77	8.40 \pm 4.22
PHBI							0.10 \pm 0.22		
POPR		1.20 \pm 1.10	4.00 \pm 5.48	0.60 \pm 1.11	0.12 \pm 0.27	2.00 \pm 2.55	8.39 \pm 10.63	10.75 \pm 5.92	7.60 \pm 10.50
RABI	2.45 \pm 1.59	3.64 \pm 7.32		2.21 \pm 1.44	1.97 \pm 0.94		7.55 \pm 5.92	1.58 \pm 1.26	2.60 \pm 4.22
RASE									0.20 \pm 0.45
RIMA				0.10 \pm 0.22	0.17 \pm 0.35		0.66 \pm 0.94	1.72 \pm 1.01	0.40 \pm 0.22
RUAC		0.13 \pm 0.30		2.00 \pm 3.66	0.16 \pm 0.23	0.92 \pm 1.02	7.25 \pm 3.89	19.30 \pm 13.01	25.00 \pm 7.91
SAPR								0.06 \pm 0.13	0.20 \pm 0.27
SELE									0.60 \pm 0.89
SEVU				3.40 \pm 7.60		0.76 \pm 1.30		1.25 \pm 2.02	
STME					0.92 \pm 1.74	1.60 \pm 2.30		0.50 \pm 1.12	
TAGI									0.10 \pm 0.22
TAOF	19.74 \pm 16.93	1.07 \pm 1.32	0.20 \pm 0.45	8.40 \pm 5.98	2.92 \pm 1.19	4.40 \pm 4.51	15.22 \pm 8.53	11.15 \pm 3.31	7.80 \pm 2.17
TRSP	0.52 \pm 0.72	0.43 \pm 0.43	0.30 \pm 0.67	7.58 \pm 7.75	2.14 \pm 0.85	10.20 \pm 5.89	11.35 \pm 6.24	9.45 \pm 5.19	3.80 \pm 3.49
UNLE	11.19 \pm 7.78	3.58 \pm 5.60	1.20 \pm 2.14	12.10 \pm 16.58	3.18 \pm 2.03	0.20 \pm 0.28	1.01 \pm 0.79	3.87 \pm 4.05	1.00 \pm 1.00
VESE				0.17 \pm 0.38	0.02 \pm 0.04		0.40 \pm 0.89	0.01 \pm 0.03	
VIMA				3.40 \pm 7.60	0.84 \pm 1.88			0.17 \pm 0.26	0.10 \pm 0.22
Mosses	8.45 \pm 3.04	26.94 \pm 19.92	58.70 \pm 23.25	4.90 \pm 5.00	4.86 \pm 2.38	24.20 \pm 7.36	0.77 \pm 0.98	1.06 \pm 1.31	1.10 \pm 0.22

Table 3. Two-way ANOVA results for forest floor cover (%) of understory plant species (group, origin and total), bare soil and debris on the studied *Nothofagus pumilio* forests, considering forest condition (PF, primary forests without previous harvesting; RH, recent harvested stands; OH, old harvested stands) and site quality (H, high; M, medium; L, low) as main factors. There are showed means \pm standard error

Factor	Dicots	Monocots	Ferns	Mosses	Natives	Exotics	Total	Bare soil	Debris
<i>A = forest condition</i>									
PF	22.39 \pm 4.74 a	4.25 \pm 1.18 a	1.90 \pm 0.82 b	5.79 \pm 0.78 c	29.35 \pm 4.93 a	4.98 \pm 2.17 a	34.33 \pm 6.11 a	43.33 \pm 6.80 c	22.33 \pm 1.45 a
RH	42.53 \pm 3.75 b	9.39 \pm 1.99 a	0.23 \pm 0.09 a	3.31 \pm 0.62 b	45.74 \pm 2.66 b	6.70 \pm 2.21 a	55.47 \pm 3.71 b	13.20 \pm 1.65 b	31.33 \pm 2.90 b
OH	49.95 \pm 2.18 c	20.35 \pm 2.00 b	0.43 \pm 0.02 a	0.45 \pm 0.11 a	45.77 \pm 2.48 b	25.46 \pm 2.84 b	71.20 \pm 1.66 c	6.80 \pm 1.16 a	22.00 \pm 1.60 a
F (2,36), <i>p</i>	55.17, <0.001	24.55, <0.001	9.09, <0.001	25.86, <0.001	20.50, <0.001	36.92, <0.001	84.65, <0.001	113.98, <0.001	11.47, <0.001
<i>B = site quality</i>									
H	46.50 \pm 2.03 c	14.61 \pm 2.65 b	1.98 \pm 0.81 b	2.51 \pm 0.69	52.50 \pm 2.08 c	13.10 \pm 2.34	65.60 \pm 1.85 c	9.40 \pm 1.49 a	25.00 \pm 1.89
M	38.90 \pm 4.57 b	11.15 \pm 2.48 ab	0.56 \pm 0.20 b	3.12 \pm 1.01	40.32 \pm 3.24 b	13.41 \pm 2.65	53.73 \pm 5.20 b	22.27 \pm 5.92 ab	24.00 \pm 1.48
L	29.48 \pm 5.91 a	8.23 \pm 2.11 a	0.03 \pm 0.02 a	3.93 \pm 0.67	28.05 \pm 3.76 a	13.62 \pm 4.62	41.67 \pm 7.20 a	31.67 \pm 7.05 b	26.67 \pm 3.33
F (2,36), <i>p</i>	19.71, <0.001	3.70, 0.034	11.15, <0.001	1.83, 0.175	34.16, <0.001	0.02, 0.979	35.42, <0.001	37.42, <0.001	0.74, 0.483
F interaction A \times B									
(4,36), <i>p</i>	20.39, <0.001	1.06, 0.389	12.93, <0.001	2.80, 0.040	3.95, 0.009	10.81, <0.001	19.92, <0.001	25.12, <0.001	9.42, <0.001

F(df), *p*: Fisher test, with degree of freedom between parentheses, with associated probability. Letters in each column show differences by Tukey test at *p* = 0.05.

independently of the forest condition (Fig. 1), meanwhile M and L were greater influenced by forest condition. In general terms, total and dicot covers increased gradually with harvesting and time, being approximately 60%-90% greater in RH than in PF, and 100%-125% greater in OH than in PF; meanwhile, native cover increased abruptly with harvesting, and then remained invariable (approx. 50% higher in harvested stands than in PF). Likewise, improvement of stand site quality directly and gradually influenced dicots and native covers, being 30%-45% significantly greater in M than in L, and 20%-30% greater in H than in M. Total understory plant cover was different among site qualities for PF, but not for RH (M = H) neither for OH (H = M = L).

For fern cover, interaction graphic showed highest values in PF-H compared to other site qualities and forest conditions (Fig. 1), and except in H, where fern cover diminished with harvesting (approx. six fold less cover in harvested stands than in PF), fern cover remained stable after cuts in the site qualities. In moss cover, interaction graphic demonstrated high similar values in PF and low values in harvested stands independently of the site qualities except for RH-L, which had approx. two fold greater moss cover than other harvested and site quality stands (Fig. 1).

For exotic cover, highest values were observed in OH-L compared to other site qualities and forest condi-

tions (Fig. 1). In general terms, exotic covers needed more time to react, remaining more similar between PF and RH and increasing approx. 400% in OH, and without clear influence of site quality. In bare soil cover, interaction responded to similar values in H independently of the forest conditions (Fig. 1), meanwhile M and L greatly diminished from PF to harvested stands (70% less in RH and 85% less in OH compared to PF). Finally, interaction in debris cover showed highest values in RH-L compared to other site qualities and forest conditions (Fig. 1).

Monocot cover did not present interactions (Table 3), and was independently influenced by both forest condition and site quality. Monocot cover needed time to change, remaining similar between PF and RH, and increasing 125% in OH; while it was 80% greater in H than in L, but without differences with M. Species with greatest changes in cover were *Osmorhiza chilensis*, *C. fontanum*, *R. acetosella* and *Galium aparine* in dicot group, and *Phleum alpinum*, *Trisetum spicatum* and *Bromus unioloides* in monocot group (Table 2).

Understory plant species richness significantly changed with forest condition and site quality of the stands (Table 4), and interactions were significant only for ferns and native species richness. In ferns, richness decreased with harvesting and time in H, while remained similar in M and L for all forest conditions (Fig. 1). In native species, richness was similar for different

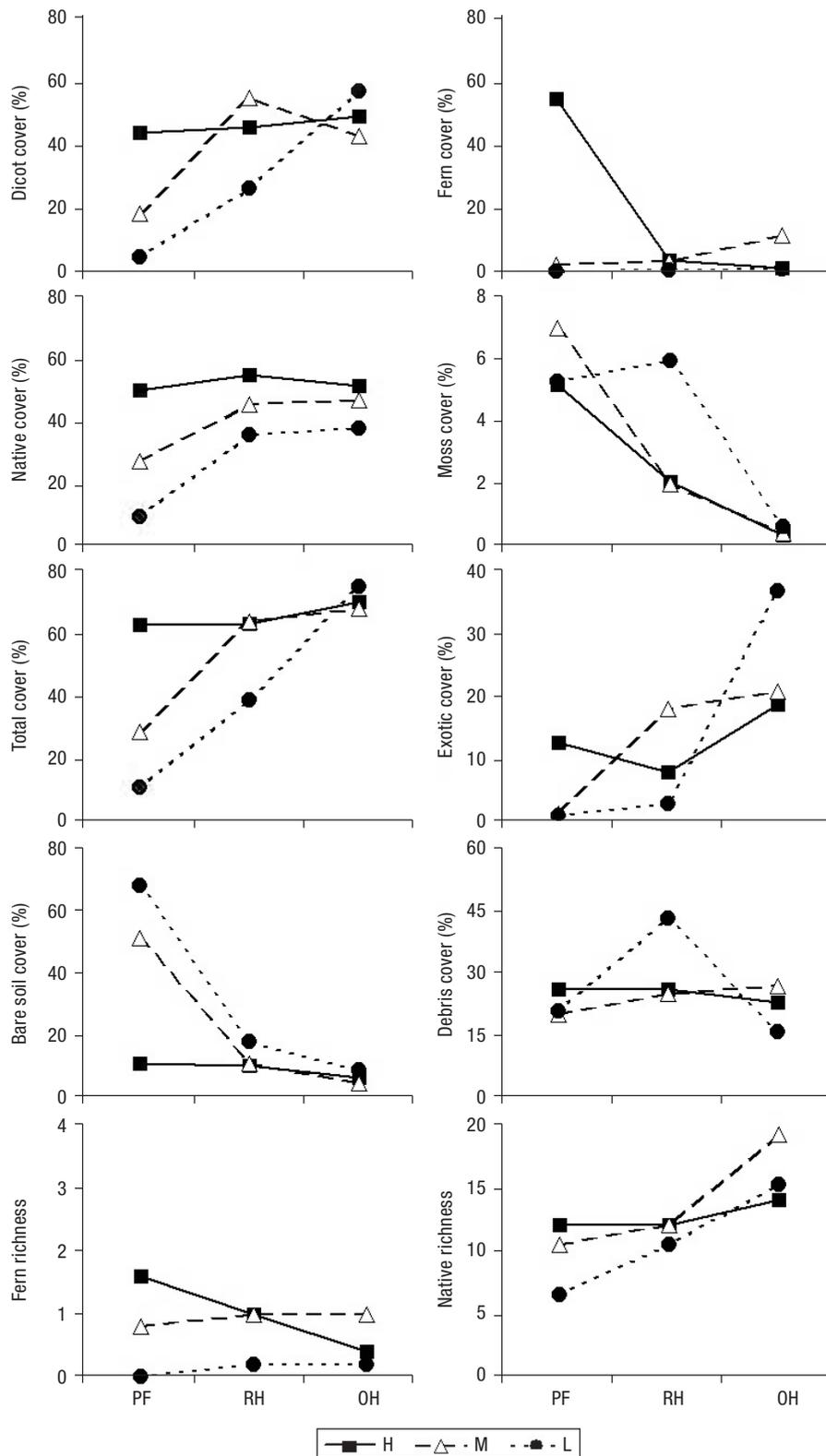


Figure 1. Understory plant species cover and richness for variables with interactions in two-way ANOVA results (see Table 3) between forest condition (PF, primary forests without previous harvesting; RH, recent harvested stands; OH, old harvested stands) and site quality (H, high; M, medium; L, low) on *Nothofagus pumilio* forests.

Table 4. Two-way ANOVA results for understory plant species richness (group, origin and total) of the studied *Nothofagus pumilio* forests, considering forest condition (PF, primary forests without previous harvesting; RH, recent harvested stands; OH, old harvested stands) and site quality (H, high; M, medium; L, low) as main factors. There are showed means \pm standard error

Factor	Dicots	Monocots	Ferns	Total	Native	Exotic
<i>A=forest condition</i>						
PF	6.9 \pm 0.6 a	3.7 \pm 0.3 a	0.8 \pm 0.2	11.4 \pm 0.9 a	9.8 \pm 0.8 a	1.6 \pm 0.2 a
RH	9.3 \pm 0.5 b	4.8 \pm 0.4 a	0.7 \pm 0.2	14.9 \pm 0.8 b	11.6 \pm 0.5 a	3.2 \pm 0.4 b
OH	12.8 \pm 0.8 c	7.7 \pm 0.3 b	0.5 \pm 0.2	21.1 \pm 1.1 c	16.3 \pm 0.9 b	4.7 \pm 0.3 c
F (2,36), <i>p</i>	26.63, <0.001	35.94, <0.001	0.81, 0.451	35.07, <0.001	28.95, <0.001	23.04, <0.001
<i>B=site quality</i>						
H	9.3 \pm 0.4 ab	5.3 \pm 0.5	1.0 \pm 0.2 b	15.6 \pm 0.8 ab	12.8 \pm 0.5 ab	2.7 \pm 0.4
M	11.0 \pm 1.1 b	5.7 \pm 0.6	0.9 \pm 0.2 b	17.7 \pm 1.6 b	14.1 \pm 1.2 b	3.6 \pm 0.4
L	8.8 \pm 0.9 a	5.2 \pm 0.6	0.1 \pm 0.1 a	14.1 \pm 1.5 a	10.8 \pm 1.1 a	3.3 \pm 0.5
F (2,36), <i>p</i>	4.11, 0.024	0.63, 0.536	9.81, <0.001	4.62, 0.016	6.68, 0.003	1.79, 0.181
F interaction A \times B (4,36), <i>p</i>	1.94, 0.125	1.11, 0.367	4.40, 0.005	2.26, 0.081	3.73, 0.012	0.33, 0.853

F(df), *p*: Fisher test, with degree of freedom between parentheses, with associated probability. Letters in each column show differences by Tukey test at *p*=0.05.

forest conditions at H, but increased with harvesting and time in M and L (Fig. 1). For other richness variables, general trends showed an increasing with harvesting and time (Table 4). Monocot richness in PF (similar to RH) was duplicated in OH, meanwhile dicot, total and exotic richness increased gradually with harvesting and time, being approx. 30%-100% greater in RH than in PF, and 85%-195% greater in OH than in PF (Table 4). On the other hand, site quality did not significantly influence monocot and exotic richness, but differences were observed for dicots and total

richness, which were approx. 25% higher in M than in L, with intermediate values in H (Table 4).

In cluster analysis (Fig. 2), three main groups were observed at 70% remaining information, which were represented by each forest condition (PF, RH and OH). At a greater distance (45% information remaining), harvested stands of RH and OH groups were combined, showing greater similarities between themselves than with PF. Old harvested stands was the most conspicuous group, while PF was the most dissimilar one, with a very low distance between M and L site quality

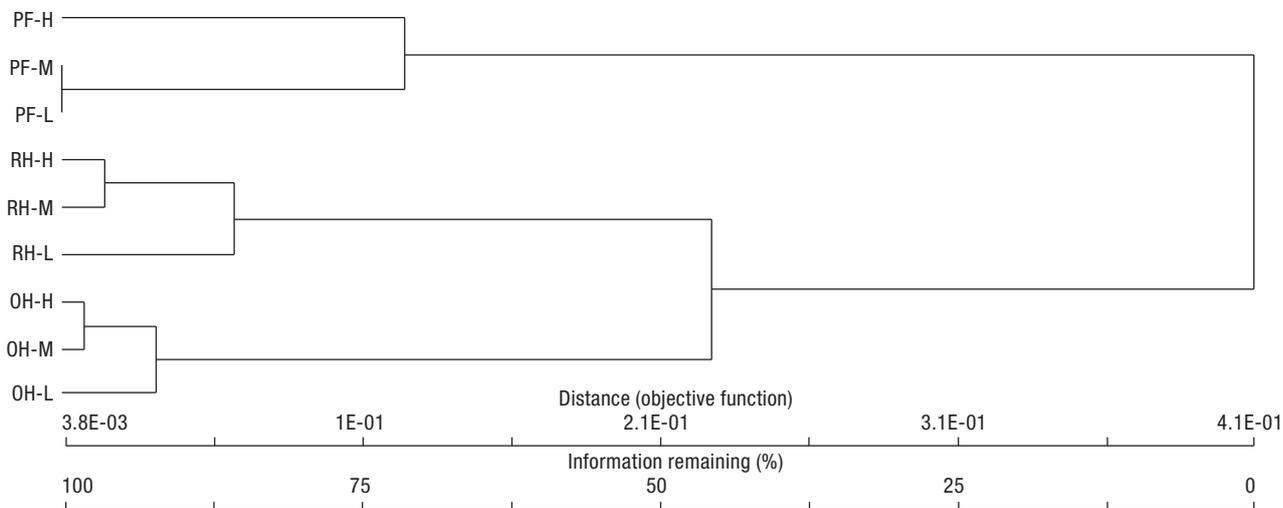


Figure 2. Cluster analysis based on understory plant species cover of the studied *Nothofagus pumilio* forests, classifying plots by forest condition (PF, primary forests without previous harvesting; RH, recent harvested stands; OH, old harvested stands) and site quality (H, high; M, medium; L, low).

stands, and a large distance among these and H site quality stands. In harvested stands, M and H were more similar between themselves than to L site quality stands. Analysis of MRPP among the three cluster groups was significant ($p = 0.001$).

Ordination graphics by reciprocal averaging showed patterns among understory plant species, forest conditions and site qualities, which were related to the life form and the origin of plant species. For forest condition, reciprocal averaging showed exotic species more related to harvested stands (Fig. 3a), and compared with site qualities, exotic species were uniformly distributed among H, M and L (Fig. 3c). However, exotic species did not occupy the same site quality or forest

condition than natives for the same genus: exotic *Cerastium fontanum* were strongly associated with M, but native *C. arvense* were more common in H and L. Similarly, *Senecio vulgaris* was found in RH and better site qualities, but *S. leucomallus* was only located in OH and L. Contrary, *Agrostis stolonifera* and *A. flavidula* shared OH areas but in different quality site stands (*A. stolonifera* in L and *A. flavidula* in M and H). Respect to life form (Fig. 3b), reciprocal averaging for forest conditions showed caespitose and rhizomatous grasses more related to both harvested stands, while shrubs were better represented only in OH except for *Berberis buxifolia*, which had greater and similar cover in PF and RH. Among site qualities, prostrate herbs were

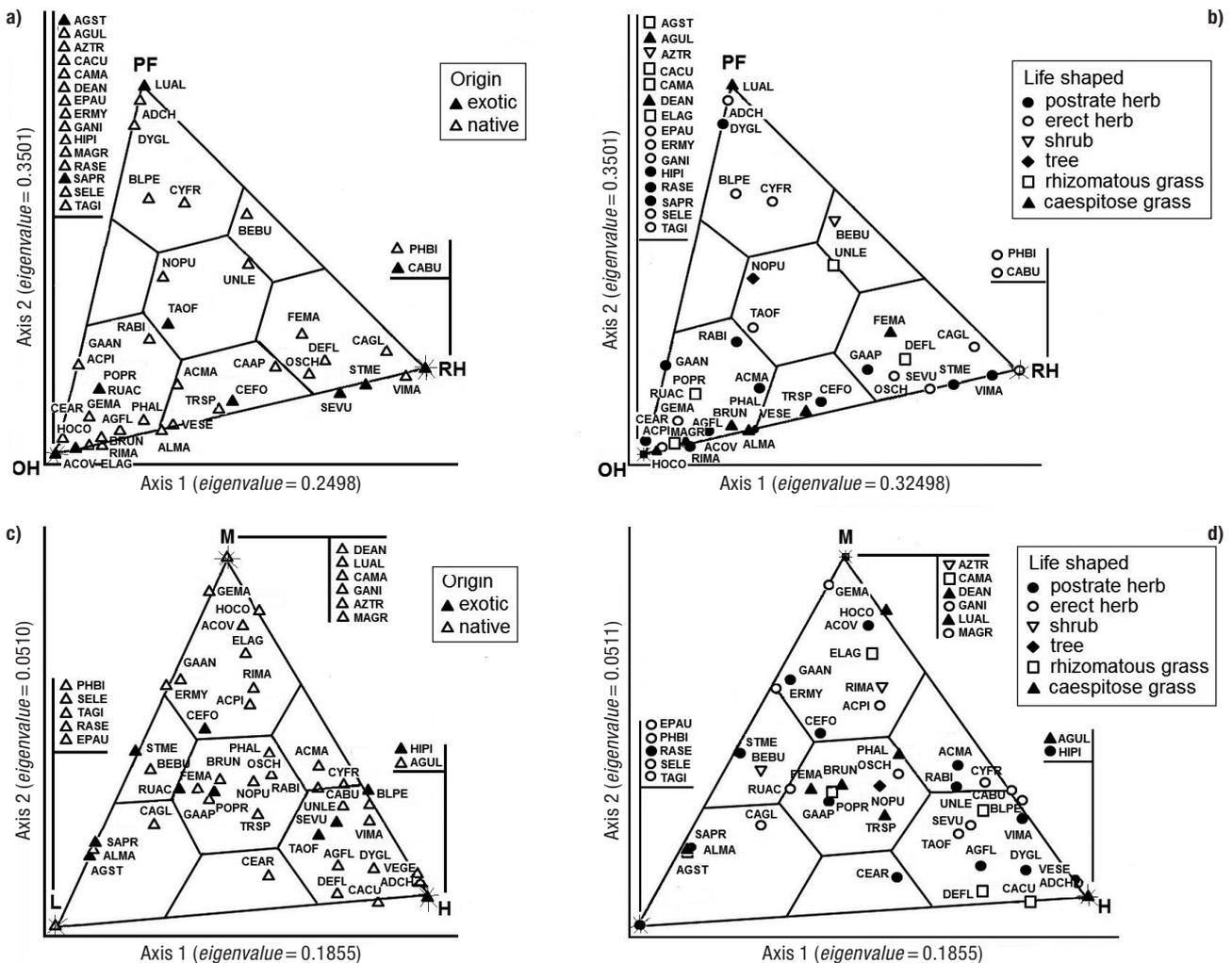


Figure 3. Reciprocal averaging analysis based on understory plant species cover of the studied *Nothofagus pumilio* forests: (i) with plots grouped by forest condition (PF, primary forests without previous harvesting, RH, recent harvested stands; OH, old harvested stands) and species classified by (a) origin and (b) life shape, and (ii) with plots grouped by site qualities (H, high; M, medium; L, low) and species classified by (c) origin and (d) life shape. Polygons inside triangles grouped species more related to one (near a vertex), two (over a side of the triangle) or all (in the middle) forest condition or site qualities.

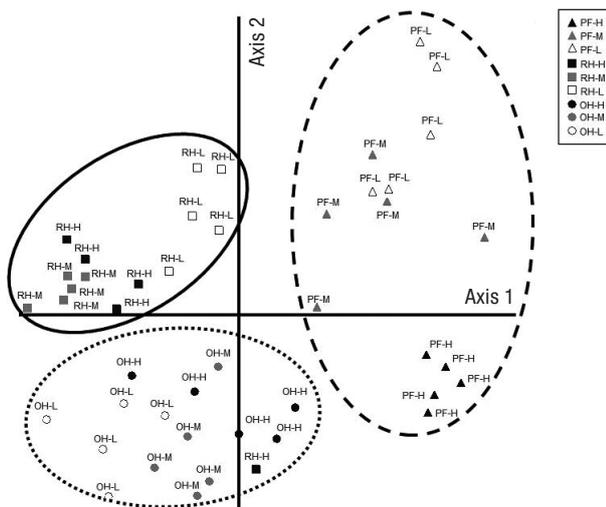


Figure 4. Non-metric multidimensional scaling based on understory plant species cover of the studied *Nothofagus pumilio* forests, with plots classified by forest condition (PF, primary forests without previous harvesting; RH, recent harvested stands; OH, old harvested stands) and site qualities (H, high; M, medium; L, low) of the stands.

dominant in H and M quality sites (Fig. 3b and 3d), as well as rhizomatous grasses were better represented in H. Distribution of *N. pumilio* regeneration was not conditioned by site quality of the stands neither forest conditions, then was located in the central area of all graphics.

Non-metrical multidimensional scaling (final stress: 20.82) complemented cluster and reciprocal averaging analyzes. Three groups were split according to forest conditions (PF, RH and OH), and within each group, site quality of the stands were separated. Only one plot of RH-H treatment was located in OH group, due to their great internal diversity. Primary forest was the most different group, and also more dispersed in axes 2, contrary to the groups of harvested forests (RH and OH) that were more concentrated. Axis 1 maximized differences in forest conditions, while axes 2 were more related to site qualities and years after cutting. Analysis of MRPP among the three NMS groups was significant ($p < 0.001$).

Discussion

Understory plant species diversity in *N. pumilio* forests is significantly affected by shelterwood and time since cuts occur, which allow the introduction of native and exotic species and increasing of dicot and monocot

covers. Species introduction after shelterwood application is also observed in other temperate forests of the world (e.g., Quinby, 2000; Poorbabaei and Poor-Rostam, 2009), and could be a consequence of other human activities too, like livestock (e.g., Ewald, 2000). In South Patagonia, plant dispersion is facilitated mainly by wind (anemochore species) or animals (zoochore species). This last could be carry out by native and domestic large herbivores, which are attracted by greater food availability in harvested stands (Martínez Pastur *et al.*, 1999), as well as by frugivorous and granivorous birds (Lencinas *et al.*, 2009). There is only one large native herbivore in Tierra del Fuego (*Lama guanicoe*, a camelid), which brows freely in all ecosystems, while domestic herbivores (mainly cattle and sheep) are usually free-ranging and feeding in open habitats such as grass and shrublands, as well as *Nothofagus* forests (Soler Esteban *et al.*, 2012).

In *Nothofagus* forests, changes in understory cover and richness are mainly allowed by the modification of ecological conditions, as microclimatic factors and resource availability at the understory level (e.g., radiation and effective rainfall) (Caldentey *et al.*, 2005; 2009). The introduction of species occurs from associated environments (grasslands, peat-lands and *Nothofagus antarctica* (Forster f.) Oersted forests, as was described by Lencinas *et al.*, 2008a), and then they remain in the system along the complete forest cycle (Martínez Pastur *et al.*, 2002). Ecological modifications can favor native and exotic understory plant species, previously present in primary forest or not, which improves growth and could produce more than two fold greater cover in open forests compared to closed stands (Lencinas *et al.*, 2011). Some exotic species (*A. stolonifera*, *C. fontanum*, *P. pratensis*, *R. acetosella* and *V. serpyllifolia*) are naturalized and grow freely in both disturbed and undisturbed communities (Moore, 1983), due to their ability to disperse and acclimatize. Anemochore exotic species, like *T. officinale* and *H. pilosella*, increase their frequency in windy areas (Lencinas *et al.*, 2008a), while *C. bursa-pastoris*, *S. procumbens*, *S. vulgaris* and *S. media* occur mainly in disturbed soils (Moore, 1983).

In many understory plant groups and species of *N. pumilio* forests, higher richness and covers are related to time transcurred after shelterwood cuts (with higher values in OH than in RH). Facilitation of introductions with time since disturbance could be related to rapid invasion of early successional species (Arnott and Beese, 1997), which are favored by differences in soil texture and chemistry due to less litter incorporation

into the forest floor (Økland *et al.*, 1999), which derived in lesser organic matter decomposition. Also, presence of newly exposed soil by litter removal generated by skidders or log movement during harvesting, could favor ruderal (defined as species that are first to colonize disturbed lands) introduction, as was observed in tips and mounds that show a high proportion of annual/biennial plants (Palmer *et al.*, 2000). Ruderal species could affect recruitment of *N. pumilio* regeneration by competitions by niches and resources, which is more problematic in OH than in RH. The shift from weedy invaders to residual species would be expected to occur with time, depending on the origin of propagules, phenological traits and potential for vegetative expansion (Halpern, 1989). Introduction of species and increasing in understory growth were greater in L stands, probably due to greater changes in microclimate conditions after harvesting and lower competition with poorer original plant communities, which could make more difficult the stand regeneration after cuts.

On the other hand, shelterwood cuts of *N. pumilio* forests produce local extinctions (*e.g.*, *L. alopecurus*) of extremely sensitive understory species. This is also observed in boreal forests (Quinby, 2000). The absence of a particular species in post-harvesting years may be attributed to harvesting impacts on microclimatic and site conditions, but also to natural variations in plant life history characteristics, or a combination of these factors (Smith *et al.*, 2008). Species classified as locally extirpated may have been dormant or simply not detected in the post-harvest sampling years (Halpern *et al.*, 2005). This could be the explanation for some absences in RH that newly appear in OH (*e.g.*, *Dysopsis glechomoides*, *C. arvensis*), although some other species could be able to re-colonize harvested areas with time, independently of the stand site quality (*e.g.*, *P. alpinum* and *Acaena magellanica*).

Other species that initially persist after disturbance may be gradually extirpated, as a result of disturbance-related stress, inability to adapt to microclimate changes, and increased competition with ruderal species (Halpern *et al.*, 2005). Also, removal of retained overstory during final cuts under shelterwood system could increase changes in microclimate, and then accelerate sensitive species extirpation. An indicator of gradual loss could be the decreasing in relative abundance of species (*e.g.*, *Uncinia lechleriana*) or groups (mosses and ferns), both showed as sensitive entities in other studies too (Lencinas *et al.*, 2008b, 2011). Increasing in moss cover in RH-L (when general trend is to dimi-

nish with harvesting) could be explained by quickly establishment of bryophyte early-successional species, similarly to the observed by Ruokolainen and Salo (2006) in Finnish forest. It is possible to found similar effects in ferns, although *Blechnum penna-marina* could also be observed in other humid open habitats, like meadows and *N. antarctica* forests (Lencinas *et al.*, 2008a).

Usually, sensitive species to disturbances often have narrow requirements for habitat conditions (Gilliam, 2007) and frequently are present at naturally low frequencies in primary forests (*e.g.*, <9% reported by Smith *et al.*, 2008); therefore, they have more probability to be affected by forest management practices. But, in primary *N. pumilio* forests, sensitive species may actually present high frequencies (*e.g.*, 100% frequency for *U. lechleriana* in some plots of primary forests). The loss of these species could be originated by their patchy distribution, *e.g.* in patches of deep shade and cool, moist, and relatively stable ground-layer microclimates (Chen *et al.*, 1993). Specific micro-environmental conditions under closed canopies are usually found in *Nothofagus* forests, *e.g.* pits, mounds, protected areas under large debris, close or far to big trees, rotten wood of dead trees, small gaps (Lencinas *et al.*, 2008b; Martínez Pastur *et al.*, 2012). At a greater scale, continuous presence of sensitive species on the landscape are usually related to variations in old-growth qualities of forests (Ohlson *et al.*, 1997), as gap presence and tree-layer structure, availability of snags and dead wood of various sizes and decay stages. Notice that old-growth qualities could differ in different forests of the world, *e.g.*, multi-specific overstory is an old-growth condition in many forests of the world, but does not exist in primary or secondary *N. pumilio* forests.

In primary and shelterwood harvested *N. pumilio* forests, understory plant richness and cover shows strong and direct correlation with the site quality of the stands (mainly dicot cover), and this was inversely correlated with mosses and exotics. Positive and negative association of vascular plant species with site quality also has been observed in other forests too (Warner and Harper, 1972; Small and McCarthy, 2005). In Tierra del Fuego, site quality of the stands is mainly determined by abiotic factors (*e.g.*, soil nutrient contents, soil drainage and depth, slope, aspect, topography and wind exposure) (Martínez Pastur *et al.*, 1997), which influence both overstory structure and understory diversity (Martínez Pastur *et al.*, 2002). High soil moisture and light availability also increase southern

Patagonian understory diversity (e.g., riparian forests and wetlands forests) (Lencinas *et al.*, 2008a; Veblen *et al.*, 1979), as does habitat and microenvironment diversity (e.g., pits and mounds, rocks, and woody debris in the forest floor) (Martínez Pastur *et al.*, 2002). Understory plant species assemblage could present a nested pattern as a consequence of their distribution in nested micro-habitats, which implies rich patches will support nearly all species, and poor patches, only generalists (Honnay *et al.*, 1999). Patchy distribution could explain different trends among site qualities in total richness ($M > L > H$) vs. average richness ($M > H > L$), mainly in less frequent and rare species, as well as introduction of species from associated environments (e.g., *Phaiopleps biflora*). Moreover, in low quality forests, with low average understory richness, generalist species are the common available source of propagules to colonize stands after disturbance. This could explain the high moss cover in L-RH, where the great availability of suitable microenvironments and substrates (reflected in higher bare soil and debris cover) was quickly occupied for bryophyte establishment after harvesting (Lencinas *et al.*, 2008b). Moreover, mosses are benefited by lower competition with native vascular plants for water and light at understory level in L compared to M and H stands, although exotic plants also are favored.

Interactions between main factors (forest conditions and site quality of the stands) are mostly explained by different responses of studied variables in H vs. M = L for different forest conditions. In H stands, where greater richness and cover by groups are observed, sensitive old-growth species (e.g., ferns) are more affected by harvesting, meanwhile ruderal introduction and increasing cover of generalist species are lower and smoothed by competition with other species of their original richest plant communities.

Nothofagus pumilio forest management by shelterwood cuts, mainly applied to meet timber objectives, homogenizes canopy structure (Martínez Pastur *et al.*, 2000) and microclimatic conditions (Caldentey *et al.*, 2009), reduces microenvironments, and gradually since harvesting increase similarity among understory of different site quality stands. This was observed in the NMS ordination (Fig. 4) where conspicuous groups are formed among R-H and M plots, as well as among OH-H, M and L plots. As was discussed previously, environmental heterogeneity and microhabitat preservation are important for the maintenance of local species diversity in the forest understory, not only for fre-

quent but also rare species or specific functional groups. Managing landscapes for a greater range of habitat conditions may, therefore, be essential for some organisms (Mitchell and Beese, 2002). Following that, shelterwood cuts in *N. pumilio* forests should generate heterogeneity at understory level, which could be achieved, for example, with more irregularity and patchiness in the retained overstory. Moreover, preservation of original understory community patches inside shelterwood harvested *N. pumilio* forests could better conserve sensitive understory plant diversity for mitigation of shelterwood impacts, as well as to provide propagules of late-seral species to re-colonize harvested stands. On the other hand, different site quality stands must received differential attention in the implementation of conservation strategies, since medium quality sites with greater diversity are typically harvested (and impacted) with great intensity. Contrarily, utility of worst quality sites as protection areas or reserves must be revised since these did not home the whole diversity of the original *N. pumilio* understory plant communities.

Conclusion

Forest management planning must consider differential impacts of shelterwood cuts depending on site quality of the stands and time transurred since harvesting occurs. For this, different site quality stands should received differential attention during the development of conservation strategies, as well as variations in shelterwood implementation (as irregularity and patchiness) should be considered to better promote understory plant species conservation inside managed areas.

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References

- Arnott JT, Beese WJ, 1997. Alternatives to clear-cutting in British Columbia coastal montane forests. *Forest Chron* 73: 670-678.

- Barrera MD, Frangi JL, Richter LL, Perdomo MH, Pinedo LB, 2000. Structural and functional changes in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina. *J Veg Sci* 11: 179-188.
- Brososke KD, Chen J, Crow TR, 2001. Understory vegetation and site factors: implications for a managed Wisconsin landscape. *For Ecol Manage* 146, 75-87.
- Caldentey J, Ibarra M, Hernández J, 2001. Litter fluxes and decomposition in *Nothofagus pumilio* stands in the region of Magallanes, Chile. *For Ecol Manage* 148: 145-157.
- Caldentey J, Ibarra M, Promis A, 2005. Microclimatic variations in a *Nothofagus pumilio* forest caused by shelterwood systems: results of seven years of observations. *Int For Rev* 7: 46.
- Caldentey J, Mayer H, Ibarra M, Promis A, 2009. The effects of a regeneration felling on photosynthetic photon flux density and regeneration growth in a *Nothofagus pumilio* forest. *Eur J For Res* 128: 75-84.
- Chen J, Franklin JF, Spies TA, 1993. Contrasting microclimates among clear-cut, edge, and interior of old-growth Douglas-fir forest. *Agric For Meteorol* 63: 219-237.
- Correa MN, 1969-1998. Flora Patagónica. Colección Científica INTA Tomo 8. Partes II, III, IVb, V, VI y VII. Buenos Aires, Argentina.
- Ewald J, 2000. Long-term impact of forest pasture on the understorey of mountain forests in the Tegernsee Alps (Bavaria). *Z Ökologie u Naturschutz* 9: 161-170.
- Fitter AH, Hay RKM, 1983. Environmental Physiology of Plants. Academic Press, London, United Kingdom. 355 pp.
- Gilliam FS, 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience* 57: 845-858.
- Haight R, 1995. Comparing extinction risk and economic cost in wildlife conservation planning. *Ecol Appl* 5(3): 767-775.
- Halpern CA, 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. *Ecology* 70: 704-720.
- Halpern CB, McKenzie D, Evans SA, Maguire DA, 2005. Initial responses of forest understoreys to varying levels and patterns of green-tree retention. *Ecol Appl* 15: 175-195.
- Honnay O, Hermy M, Coppin P, 1999. Nested plant communities in deciduous forest fragments: species relaxation or nested habitats? *Oikos* 84: 119-129.
- Kent M, Coker P, 1992. Vegetation description and analysis: a practical approach. CRC Press-Belhaven Press, London, United Kingdom. 363 pp.
- Lencinas MV, Martínez Pastur G, Rivero P, Busso C, 2008a. Conservation value of timber quality *versus* associated non-timber quality stands for understory diversity in *Nothofagus* forests. *Biodiv Conserv* 17: 2579-2597.
- Lencinas MV, Martínez Pastur G, Solán R, Gallo E, Cellini JM, 2008b. Forest management with variable retention impact over bryophyte communities of *Nothofagus pumilio* understory. *Forstarchiv* 79: 77-82.
- Lencinas MV, Martínez Pastur G, Gallo E, Cellini JM, 2009. Alternative silvicultural practices with variable retention improve bird conservation in managed South Patagonian forests. *For Ecol Manage* 258: 472-480.
- Lencinas MV, Martínez Pastur G, Gallo E, Cellini JM, 2011. Alternative silvicultural practices with variable retention to improve understory plant diversity conservation in southern Patagonian forests. *For Ecol Manage* 262: 1236-1250.
- Martínez Pastur G, Peri P, Vukasovic R, Vaccaro S, Piriz Carrillo V, 1997. Site index equation for *Nothofagus pumilio* Patagonian forest. *Phyton* 6: 55-60.
- Martínez Pastur G, Peri P, Fernández C, Staffieri G, Rodríguez D, 1999. Desarrollo de la regeneración a lo largo del ciclo del manejo forestal de un bosque de *Nothofagus pumilio*: 2. Incidencia del ramoneo de *Lama guanicoe*. *Bosque* 20: 47-53.
- Martínez Pastur G, Cellini J, Peri P, Vukasovic R, Fernández C, 2000. Timber production of *Nothofagus pumilio* forests by a shelterwood system in Tierra del Fuego (Argentina). *For Ecol Manage* 134: 153-162.
- Martínez Pastur G, Peri P, Fernández MC, Staffieri G, Lencinas MV, 2002. Changes in understory species diversity during the *Nothofagus pumilio* forest management cycle. *J For Res* 7: 165-174.
- Martínez Pastur G, Cellini JM, Peri P, Lencinas MV, Gallo E, Soler Esteban R, 2009. Alternative silviculture with variable retention in timber management of South Patagonia. *For Ecol Manage* 258: 436-443.
- Martínez Pastur G, Peri P, Cellini JM, Lencinas MV, Barrera M, Ivancich H, 2011a. Canopy structure analysis for estimating forest regeneration dynamics and growth in *Nothofagus pumilio* forests. *Ann For Sci* 68: 587-594.
- Martínez Pastur G, Cellini JM, Lencinas MV, Barrera M, Peri PL, 2011b. Environmental variables influencing regeneration of *Nothofagus pumilio* in a system with combined aggregated and dispersed retention. *For Ecol Manage* 261: 178-186.
- Martínez Pastur G, Jordán C, Soler Esteban R, Lencinas MV, Ivancich H, Kreps G, 2012. Landscape and microenvironmental conditions influence over regeneration dynamics in old-growth *Nothofagus betuloides* Southern Patagonian forests. *Plant Biosyst* 146: 201-213.
- McCune B, Mefford MJ, 1999. Multivariate analysis of ecological data. Version 4.0. MjM software. Gleneden Beach, Oregon, USA.
- Mitchell SJ, Beese WJ, 2002. The retention system: reconciling variable retention with the principles of silvicultural systems. *For Chron* 78: 397-403.
- Mittermeier RA, Mittermeier CG, Brooks TM, Pilgrim JD, Konstant WR, DA Fonseca GAB, Kormos C, 2003. Wilderness and biodiversity conservation. *Proc Nat Academy Sci* 100: 10309-10313.
- Moore DM, 1983. Flora of Tierra del Fuego. Missouri Botanical Garden, Anthony Nelson, London, United Kingdom.
- Økland R, Rydgren K, Økland T, 1999. Single-tree influence on understorey vegetation in a Norwegian boreal spruce forest. *Oikos* 87: 488-498.
- Ohlson M, Söderström L, Hörnberg G, Zackrisson O, Hermansson J, 1997. Habitat qualities versus long-term

- continuity as determinants of biodiversity in boreal old-growth swamp forest. *Biol Conserv* 81: 221-231.
- Palmer MW, Mcalister SD, Arévalo JR, Decoster JK, 2000. Changes in the understory during 14 years following catastrophic wind-throw in two Minnesota forests. *J Veg Sci* 11: 841-854.
- Poorbabaie H, Poor-Rostam A, 2009. The effect of shelterwood silvicultural method on the plant species diversity in a beech (*Fagus orientalis* Lipsky) forest in the north of Iran. *J For Sci* 55: 387-394.
- Quinby PA, 2000. First-year impacts of shelterwood logging on understory vegetation in an old-growth pine stand in central Ontario, Canada. *Environ Conserv* 27: 229-241.
- Rosenfeld JM, Navarro Cerrillo RM, Guzmán Álvarez JR, 2006. Regeneration of *Nothofagus pumilio* (Poepp. et Endl.) Krasser forests after five years of seed tree cutting. *J Env Manage* 78: 44-51.
- Ruokolainen L, Salo K, 2006. The succession of boreal forest vegetation during ten years after slash-burning in Koli National Park, eastern Finland. *Ann Bot Fennici* 43: 363-378.
- Schmidt H, Urzúa A, 1982. Transformación y Manejo de los Bosques de Lengua en Magallanes. Universidad de Chile, Santiago, Chile. *Ciencias Agrícolas* no.11. 62 pp.
- Small CJ, McCarthy BC, 2005. Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, USA. *For Ecol Manage* 217: 229-243.
- Smith KJ, Keeton WS, Twery MJ, Tobi DR, 2008. Understory plant responses to uneven-aged forestry alternatives in northern hardwood-conifer forests. *Can J For Res* 38: 1303-1318.
- Soler Esteban R, Martínez Pastur G, Lencinas MV, Borrelli L, 2012. Differential forage use between large native and domestic herbivores in Southern Patagonian *Nothofagus* forests. *Agrofore Syst* 85: 397-409.
- Veblen TT, Veblen AT, Schlegel FM, 1979. Understory patterns in mixed evergreen-deciduous *Nothofagus* forests in Chile. *J Ecol* 67: 809-823.
- Warner JH, Harper KT, 1972. Understory characteristics related to site quality for aspen in Utah. *Science Bulletin, Biological Series, Volume XVI, no. 2*, Brigham Young University, USA.