

Conservation value of timber quality versus associated non-timber quality stands for understory diversity in *Nothofagus* forests

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Abstract Conservation strategies of forested landscapes must consider biodiversity of the included site types, i.e. timber-quality forests and associated non-timber-quality stands. The objectives were to characterize forest overstory structure in timber-quality versus associated non-timber-quality stands; and to compare their understory communities. Six forest types were sampled in *Nothofagus* forests of Tierra del Fuego (Argentina): two timber-quality *N. pumilio* forests, and four associated non-timber-quality stands (edge, *N. antarctica*, wetlands and streamside forests). Overstory structure and understory vegetation (species richness, frequencies, cover and biomass) were characterized during spring and summer seasons. Analysis of variance and multivariate were carried out. Overstory structure differed across the site types, with higher tree size, canopy closure and tree volume in timber-quality stands. Fifty-one understory plant species were observed, but understory variables varied with site types, especially wetlands (highest native and exotic richness, cover and biomass, and 25% of exclusive species). Site types were grouped in three:

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N. antarctica stands, streamside stands and the other *N. pumilio* forests according to multivariate analysis. Forty three percent of plants were distributed in all site types, and all timber-quality forest understory species were present in some associated non-timber-quality stands. Timber-quality *N. pumilio* forests have a marginal value for understory conservation compared to associated non-timber-quality stands, because these last include all the plants observed in timber-quality forests and also possess many exclusive species. Therefore, protection of associated non-timber-quality stands during forest management planning could increase understory conservation at landscape level, and these could be better reserves of understory diversity than retentions of timber-quality stands.

Keywords Landscape · Forest management · *Nothofagus antarctica* · *Nothofagus pumilio* · Tierra del Fuego

Abbreviations

LF	<i>N. pumilio</i> forest on flat ground
MHLF	<i>N. pumilio</i> forest on a hillside
BLR	Edge between <i>N. pumilio</i> forest and grassland
ÑF	<i>N. antarctica</i> forest
W	<i>N. pumilio</i> – <i>N. antarctica</i> forest wetland
S	Streamside <i>N. pumilio</i> forest
BAF	Basal area factor
ANOVA	Analysis of variance
Ds	Simpson index
JQ	Jaccard index for qualitative data

Introduction

Conservation strategies of forested landscapes should consider all the biodiversity that it includes, as timber-quality forests and also other site types. Usually, forested landscapes are mosaics of different site types, where timber-quality forests rarely constitute large, continuous masses since these are mixed with associated non-timber-quality stands. Natural timber-quality forests mainly occupy the best site quality areas and yield marketable wood products. On the other hand, associated non-timber-quality stands should not be harvested, because are not profitable, have legal restrictions, or present special protective ecosystem functions, e.g. stands with low site quality due to soil impediments, excess of water or wind exposure; non-timber tree forest species; streamside forests; forest edges with roads, grasslands or peatlands; timber forests with excessive slope; grasslands and peatlands, near or into the forests.

Forest management in timber-quality stands modifies this biodiversity, and could produce species loss (Wigley and Roberts 1997; Deferrari et al. 2001; Jalonen and Vanha-Majamaa 2001; Spagarino et al. 2001; Martínez Pastur et al. 2002a). These losses could be due to changes in the forest structure, microclimatic conditions or nutrient cycles (Reader and Bricker 1992; Lewis and Whitfield 1999; Caldenty et al. 2001). However, most studies only analyze biodiversity loss in timber-quality forests (Thomas et al. 1999; Quinby 2000; Deferrari et al. 2001; Spagarino et al. 2001; Jalonen and Vanha-Majamaa 2001; Martínez Pastur et al. 2002a), without to consider the interaction with remainder site types enclosed in the landscape (Hutchinson et al. 1999; Rosso et al. 2000; Peh et al. 2006).

Plant species and understory communities are well known in temperate forest ecosystems. However, few works define understory plant diversity in each forest site type, as well as microclimatic, edaphic and ecological characteristics, or relationships among unmanaged timber-quality and associated non-timber-quality stands. For understory plant conservation, generalist species have little importance, while those that only occur in timber-quality forests could acquire greater ecological importance, due to these stand will be impacted through the implementation of silviculture practices (Martínez Pastur et al. 2002a). The objectives of this study were to: (1) characterize forest overstory structure in temperate timber-quality versus their associated non-timber-quality stands in southern Patagonia; and (2) compare composition and biomass of their understory plant species. The hypotheses are overstory structure, composition and biomass of understory species differed between site types in temperate forests of Tierra del Fuego, which influence over their conservation value.

Methods

Study site description

Nothofagus genus is the main component of the Magellanic forests, with a wide range of natural distribution from 36°50' to 55°02' SL. These forests are predominantly pure and deciduous, mainly of *N. pumilio* (lenga) and *N. antarctica* (ñire). In Tierra del Fuego, Argentina, forests are mainly used for harvesting (only over *N. pumilio* forests), cattle grazing and tourism, considering in first place economic objectives (Martínez Pastur et al. 2000) and in second place, conservative proposes (Martínez Pastur et al. 2002a) for the natural ecosystem management.

Unmanaged natural *Nothofagus* timber-quality forests and associated non-timber-quality stands were selected in central zone of Tierra del Fuego Island, Argentina, according to their good conservation status and easy field access. Forests were located at Ushuaia Ranch (54°27'32" SL, 67°30'16" WL), 10 km north to Fagnano Lake and 5 km east to Yehuin Lake (Fig. 1). Climate is characterized by short, cold summers and long, snowy and frozen winters. Mean monthly temperatures vary from about -7 to 14°C (extremes vary from -17 in July to 22°C in January). Only 3 months year⁻¹ are free of mean temperatures under 0°C , and growing season extends for about 5 months. Precipitation is near 400 mm year⁻¹ and average wind speed is 8 km h⁻¹, reaching up to 100 km h⁻¹ during storms, which eventually could produce forest blow-down in large areas (Rebertus et al. 1997).

An area of 1000 ha was chosen for sampling (20% of the ranch), because here none silvicultural practices neither intensive cattle grazing was done in the past, but natural browsing pressure of *Lama guanicoe* (guanaco) over *Nothofagus* seedlings and saplings exists (Pulido et al. 2000). Forests were classified by fieldwork identification and analysis of aerial photos (*Instituto Geográfico Militar*, February 1989, 1:20600) or satellite images (*SPOT*, February 1995). Six site types composed by several forest stands were selected for sampling along a north-south topographic gradient (Fig. 1), and were classified as:

1. Timber-quality non-sloping *Nothofagus pumilio* forest (LF), which grow on flat ground and has not been previously logged;
2. Timber-quality sloping *N. pumilio* forest (MHLF), which grow on mid-altitude southern hillside (slope of 25°) and has not been previously logged;

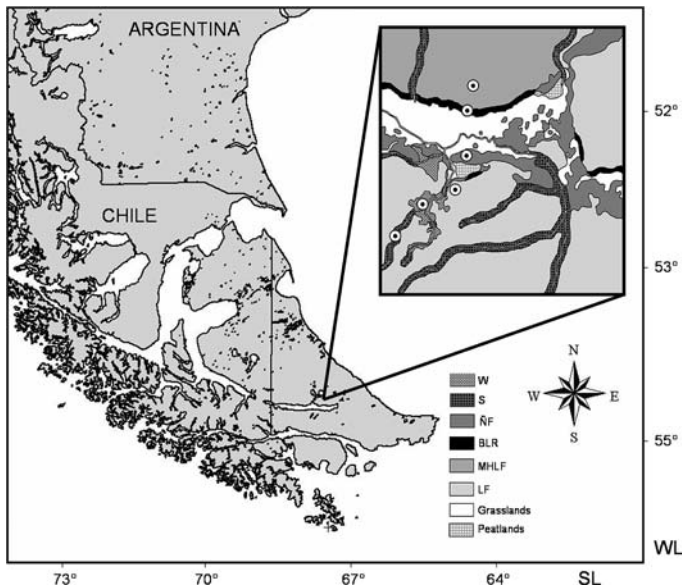


Fig. 1 Location of Tierra del Fuego Island in the Argentine southernmost extreme off the mainland, site types and location of the sampled zones (indicated with points). Site types as follows: W = *N. pumilio*–*N. antarctica* forest wetland; S = Streamside *N. pumilio* forest; ÑF = *N. antarctica* forest; BLR = Edge between *N. pumilio* forest and grassland; MHLF = *N. pumilio* forest on a hillside; LF = *N. pumilio* forest on flat ground

3. Associated non-timber-quality edge of *N. pumilio* forest (BLR) and a mesophytic low valley grassland dominated by *Festuca gracillima*;
4. Associated non-timber-quality *N. antarctica* forest (ÑF);
5. Associated non-timber-quality forested wetland (W), where flooded soil impediments exits for heavy machine transit;
6. Associated non-timber-quality streamside *N. pumilio* forest (S), which have special protective ecosystem functions.

In Tierra del Fuego, timber-quality forests are those that had at least a site quality of V (according to site quality classification of Martínez Pastur et al. 1997), that correspond to at least 15 m stand dominant height; and could produce saw-timber volumes up to 40 m³ ha⁻¹ (healthy logs up to 30 cm diameter and 3 m long).

Forest structure characterization

Each site type was characterized through ten forest plots systematically located 100 m apart, where trees were measured by point sampling method (using BAF 8) (Bitterlich 1984; Prodan et al. 1997). This method, also known as angle count sampling, was introduced half way through the last century (Bitterlich 1948). Point sampling is sampling with probability proportional to size, and tree probability selection is proportional to its basal area. A count is made of all the trees that can be seen from a point (in 360°) that have a diameter larger than a constant projected angle.

To characterize the forest structure, basal area, diameter at breast height, number of trees, dominant tree species and total over bark volume were obtained. In addition, dominant height (average of the three dominant trees closest to the sampling point centre) was

measured using a clinometer and a distance rangefinder, and canopy cover was measured by a spherical densiometer (Lemmon 1957). Site quality and volume equations were proposed previously for *N. pumilio* (Martínez Pastur et al. 1997; 2002b) and *N. antarctica* (Lencinas et al. 2002). For *N. pumilio*, stands growing in a site quality *I* could have more than $1100 \text{ m}^3 \text{ ha}^{-1}$ and tress reach more than 27.5 m height; in a site quality *II* have up to $900 \text{ m}^3 \text{ ha}^{-1}$ and heights between 24.1 and 27.5 m; in a site quality *III* have up to $700 \text{ m}^3 \text{ ha}^{-1}$ and heights between 20.5 and 24.0 m; while in a site quality *V* stands have less than $400 \text{ m}^3 \text{ ha}^{-1}$ and trees present a total height less than 17.0 m (Martínez Pastur et al. 1997, 2000; Gea et al. 2004). For *N. antarctica*, stands growing in a site quality *I* could have more than $350 \text{ m}^3 \text{ ha}^{-1}$ and tress reach more than 12.0 m height; in a site quality *II* have up to $250 \text{ m}^3 \text{ ha}^{-1}$ and heights between 10.0 and 12.0 m; in a site quality *III* have up to $175 \text{ m}^3 \text{ ha}^{-1}$ and heights between 8.0 and 10.0 m; in a site quality *IV* have up to $115 \text{ m}^3 \text{ ha}^{-1}$ and heights between 6.0 and 8.0 m; while in a site quality *V* stands have less than $60 \text{ m}^3 \text{ ha}^{-1}$ and trees present a total height less than 6.0 m (Lencinas et al. 2002).

Understory characterization

Understory was characterized in each site type during spring (November 1998) and summer (March 1999). Ten plots per season and site type ($N = 6 \text{ site types} \times 2 \text{ seasons} \times 10 \text{ plots}$) were taken, in the same stands where forest structure was measured. Each plot had four 0.25 m^2 subplots orthogonally placed 5 m apart from the centre (Martínez Pastur et al. 2002a), except in streamside forest stands. In this site type, subplots were located perpendicular to the stream, two of them in each margin, placed 2 and 3 m apart from the centre of the watercourse (Denneler et al. 1999; Treonis et al. 1999). Vascular plants (Dicotyledonae, Monocotyledonae and Pteridophytae) were taxonomically classified by species, following Moore (1983) and Correa (1969–1998), and non-vascular plants (mosses and liverworts) were considered together in the same group. Forest floor cover (woody debris, bare floor and understory species) was registered by a grid of 100 points m^{-2} in every subplot (Mueller-Dombois and Ellenberg 1974). All living aboveground plant material was collected for biomass determination, and this was dried in an oven at 70°C until constant weight. Also, studied area was checked to found other not sampled plant species in each site type, which were added to a species list to maximize diversity characterization. Then, species were classified as *sampled* when they were registered in plots or *not-sampled* when they were observed in floristic inventories but not in plots.

Data analysis

Forest structure variables, as dominant height, site quality, diameter at breast height, basal area, total over bark volume and canopy cover, did not accomplish the normality and homocedasticity assumptions of parametric analysis of variance-ANOVA. Then, these were compared among site types using non-parametric ANOVA (Kruskal–Wallis test) while median comparisons were done using confidence intervals by the median test (Payton et al. 2000).

Understory variables, as frequency, floor cover and biomass, accomplished the assumptions of parametric ANOVA. Therefore, this analysis was preferred, while mean comparisons were done by Tukey honestly significant difference test ($P < 0.05$). Previously, average frequencies of 38 understory plant species were analyzed, comparing homogeneity among seasons and site types with Chi-square tests ($P < 0.05$). These species correspond to

those sampled in 95% plots in each forest site type. For species frequency data, information of both seasons was used in one-way ANOVA, because this was homogeneous between summer and spring samplings ($P > 0.25$). For floor cover and understory biomass analyses, species data were combined in groups (tree regeneration, other dicots, monocots and lower plants), and then group values were analysed by two-way ANOVA, with seasons and site types as main factors. In the case of biomass data, it was transformed by $X = \ln(Y + 1)$ before running ANOVA, where X is the transformed variable and Y is dry biomass in kg ha^{-1} . Frequency and floor cover did not need any transformations to achieve normality and homoscedasticity assumptions.

Site types were characterized and compared through alpha, beta and gamma diversity (Moreno 2001). Alpha diversity is a specific richness measurement of a homogeneous community; beta diversity is the differentiation degree of communities along habitat gradients; and total or gamma diversity of a landscape is obtained from the alpha diversity and the beta differentiation degree among them (Whittaker 1972). Alpha diversity was evaluated by sampled specific richness and *Simpson* index, which was calculated as: $Ds = 1 - \lambda$, being $\lambda = \sum p_i^2$, with p_i as the proportional abundance of i species. Beta diversity was obtained as: $d = 1 - \text{JQ}$, where JQ is the *Jaccard* index for qualitative data calculated by $\text{JQ} = [c / (a + b - c)]$, with a as the species quantity of A site type, b the species quantity of B site type, and c the common species between A and B . About the gamma index, this was obtained by addition of average alpha and beta, which was calculated based on the *Simpson* coefficient by $\beta = \sum q_j \lambda_j - \sum P_i^2$, where $P_i = \sum q_j p_j$, with q_j as the proportional area of the j site type and P_i represent the mean frequency of the i species (p_i) in the landscape, weighted by the site type area (q_j).

Relationships among site types were studied over a biomass data matrix of the 38 more frequent understory species. Cluster analysis of the six site types was done using a Ward's method linkage and Euclidean distance measurement (Gauch and Whittaker 1981). Then, detrended correspondence analysis was done (Hill 1979; Greenacre 1984; Manly 1994), with down-weight of rare species. For multivariate analyses, Statgraphics Plus 4.0 software (Statistical Graphics Corp., Manugistics Inc., Maryland, USA) and PC-ORD program (McCune and Mefford 1999) were used. Complementary, overlap graphics analysis of species richness among cluster results was done (Willot 1999).

Results

Characterization of sampled stands

Forest structure in timber-quality and associated non-timber-quality stands mainly differed in canopy cover and total stand height (Table 1). Timber-quality stands were characterized by large trees (up to 23 m height), with a closed canopy (up to 96%) and high tree volume ($600\text{--}700 \text{ m}^3 \text{ ha}^{-1}$). These sites represented 64% study area (Fig. 1). *Nothofagus antarctica* forests, which represented 11% study area, had lesser height and total volume (55% compared to timber-quality stands) (Table 1). Also, they had less canopy cover than some timber-quality forests (MHLF) and the best site quality for the species. Edge stands and streamside forests, which represented a low percentage of the landscape (2% and 8% respectively), had very similar forest structure to timber-quality stands. In forested wetlands (2% of the area), timber and non-timber-quality species coexisted and grew in soil completely saturated by water, with the lowest canopy cover (77%). The open places (13% of the landscape) were conformed by grasslands and peatlands.

Table 1 Non-parametric ANOVA (Kruskal–Wallis test) results for forest structure variable analyses in timber quality and associated non-timber quality stands of *Nothofagus* forest in Tierra del Fuego (average ± standard error)

Variables	Site types						Kruskal–Wallis test
	W	S	NF	BLR	MHLF	LF	
Dominant tree species	<i>Nothofagus pumilio</i> – <i>N. antarctica</i>	<i>Nothofagus pumilio</i>	<i>Nothofagus antarctica</i>	<i>Nothofagus pumilio</i>	<i>Nothofagus pumilio</i>	<i>Nothofagus pumilio</i>	–
Dominant height (m)	17.6 ± 1.2c	21.4 ± 1.2b	13.5 ± 0.8c	27.2 ± 0.8a	22.7 ± 0.3b	24.2 ± 0.5ab	42.531**
Site quality (I–V)	4.25 ± 0.3a	3.1 ± 0.3bc	1.4 ± 0.2d	1.7 ± 0.2cd	2.9 ± 0.1b	2.6 ± 0.2bc	38.397***
Diameter at breast height (cm)	38.5 ± 4.1	46.6 ± 6.6	40.0 ± 4.8	41.5 ± 6.9	49.5 ± 3.6	36.5 ± 3.8	6.394 ns
Basal area (m ² ha ⁻¹)	45.4 ± 4.2	53.1 ± 3.7	48.0 ± 2.1	43.2 ± 3.3	49.2 ± 6.3	56.4 ± 2.1	2.486 ns
Total over bark volume (m ³ ha ⁻¹)	364 ± 38bc	573 ± 42ab	336 ± 14c	543 ± 49b	585 ± 76ab	682 ± 32a	17.132**
Canopy cover (%)	76.7 ± 3.4c	90.7 ± 1.9bc	92.1 ± 1.4bc	95.1 ± 1.3ab	98.0 ± 0.7a	95.7 ± 0.7b	42.775***

W = Forest wetland; S = Streamside forest; NF = *N. antarctica* forest; BLR = Edge between forest and grassland; MHLF = Forest on a hillside; LF = Forest on flat ground. In Site quality variable, *I* corresponds to the best and *V* to the worst stands. Significance levels of Kruskal–Wallis test are indicated by: * $P < 0.05$; ** $P < 0.01$; ns = Not significant. Different letters within a same row represent significant differences at $P < 0.05$ by confidence intervals for the medians

Understorey richness

Understorey specific composition varied with site type (Table 2). Wet areas presented the highest richness (41 species in wetlands and 40 in streamside forests), and MHLF had the least richness (18 species). *Non-sampled* species represented 2% to 20% of the site type richness. Exotic plant richness varied from two to nine species along the forest site types (Table 2) being minimum in MHLF and maximum in wetlands and streamside forests. *Taraxacum officinale* and *Agrostis stolonifera* were found in all site types, while *Cerastium fontanum* was only found in BLR. Both fern species (*Blechnum penna-marina* and *Cystopteris fragilis*) were present simultaneously in LF, edges, wetlands and streamside forests, while *C. fragilis* appeared alone in MHLF. All native species in timber-quality forests were present in some associated non-timber-quality stands (BLR, ÑF, W or S).

The cluster analysis allowed to arrange site types into three groups: (a) *N. pumilio* forests and wetlands, where MHLF and BLR were more similar between itself, than with LF and W; (b) streamside *N. pumilio* forests (S); and (c) *N. antarctica* forests (ÑF), which were far related to the last group at a major Euclidean distance (Fig. 2a). Richness overlap analysis showed 43% of plants species are distributed in all site types. Streamside areas had 78% of the observed richness (Fig. 2b), with 6% of exclusive species (*Agrostis uliginosa*, *Macrachaenium gracile* and *Phleum pratense*). Furthermore, *N. antarctica* stands contained 4% of unique species (*Agropyron pubiflorum* and *Deschampsia flexuosa*) (Table 2). The great number of shared species (29%) between streamside areas and the group of *N. pumilio* forests and wetlands is related with the inclusion of W in this group.

When alpha diversity was analyzed, wet areas were the most diverse site types (39 species and 0.93 *Simpson* index for S, and 38 species and 0.94 *Simpson* index for W), and MHLF forest was the least diverse (17 species and 0.81 *Simpson* index). When beta diversity was examined in combination among the six site types, the highest percentage of shared species was observed in the pair S–W (0.25 by *Jaccard* index), while the greatest dissimilarities were observed in the pairs MHLF–W, BLR–W and ÑF–W (from 0.54 to 0.66), and MHLF–S and ÑF–S (from 0.56 to 0.58). Gamma diversity reached 0.93 in the site type analysis, being intra diversity larger (0.92 of mean alpha diversity) than shared one (0.01 of beta diversity), which contributed with a small proportion.

Understorey frequency, floor cover and biomass

The most frequent species in forested landscape were *Nothofagus pumilio* seedlings, *Cardamine glacialis*, *Osmorhiza depauperata* (75–100% frequency each) and *Galium aparine* (50–75% frequency) (Table 2). When species frequency in each site type was analyzed, significant differences for twenty-three species were found ($P < 0.05$). The four most frequent species at landscape level also were the most abundant in the timber-quality forests. In contrast, *Phleum alpinum*, *Uncinia lechleriana* var. *lechleriana* and *Trisetum spicatum* presented high variability (from 0 to 80%) depending of the site type. In wet forests another species were the most frequent ones, such as *Senecio smithii* (80% frequency), *Schizeilema ranunculoides* and *Cerastium fontanum* (73% each), and *Acaena magellanica* (70%). *Festuca magellanica*, *Berberis buxifolia* and *Cotula scariosa* have frequencies up to 50% in *N. antarctica* forests.

Floor cover significantly differed between seasons and among forest site types (Table 3). Understorey cover was significantly higher (52%) in summer than in spring. Debris, lower plants and tree regeneration cover were similar between seasons ($P > 0.09$). Debris cover did not show significant differences between site types. Wetlands had the largest total

Table 2 Mean frequency of understory species in timber quality and associated non-timber quality stands of *Nothofagus* forests in Tierra del Fuego, including native/exotic status (N/E)

Species	Code	N/E	Site types						
			W	S	ÑF	BLR	MHLF	LF	
<i>Acaena magellanica</i> (Lam.) Vahl	ACMA	Native	0.80	0.75	0.20	0.45	0.15	0.20	
<i>Adenocaulon chilense</i> Less.	ADCH	Native		0.35				0.10	
<i>Agropyron pubiflorum</i> (Steudel) Parodi	AGPU	Native			P				
<i>Agrostis stolonifera</i> L.	AGST	Exotic	0.15	0.25	0.30	0.15	0.15	0.30	
<i>Agrostis uliginosa</i> Phil.	AGUL	Native		0.01					
<i>Alopecurus magellanicus</i> Lam.	ALMA	Native	0.35	0.01	P				
<i>Berberis buxifolia</i> Lam.	BEBU	Native	0.05	0.05	0.70		0.05	0.15	
<i>Blechnum penna-marina</i> (Poiret) Kuhn	BLPE	Native	0.40	0.50		0.01		P	
<i>Bromus unioloides</i> Humb., Bonpl. Et Kunth	BRUN	Native			0.01			P	
<i>Cardamine glacialis</i> (Forster f.) DC	CAGL	Native	0.75	1.00	1.00	0.95	0.95	0.90	
<i>Carex curta</i> Gooden	CACU	Native	0.40	0.45	0.65	0.15		0.40	
<i>Carex macloviana</i> D'Urv.	CAMA	Native	0.10						
<i>Cerastium fontanum</i> Baumg.	CEFO	Exotic	0.80	0.55		0.05			
<i>Chiliotrichum diffusum</i> (Forster f.) O. Kuntze	CHDI	Native				P			
<i>Colobanthus quitensis</i> (Kunth) Bartl.	COQU	Native	0.20						
<i>Cotula scariosa</i> (Cass.) Franchet	COSC	Native	0.40	0.15	0.70	0.20	0.05	0.20	
<i>Cystopteris fragilis</i> (L.) Bernh.	CYFR	Native	0.05	0.05		0.01	0.01	0.05	
<i>Deschampsia flexuosa</i> (L.) Trin.	DEFL	Native			P				
<i>Dysopsis glechomoides</i> (A. Richard) Müller Arg.	DYGL	Native	P	0.45		0.10	0.70	0.75	
<i>Epilobium australe</i> Poepp. & Hausskn. ex Hausskn.	EPAU	Native	0.10	0.05				0.05	
<i>Festuca magellanica</i> Lam.	FEMA	Native	0.30	0.30	0.95	0.35	0.20	0.45	
<i>Galium antarcticum</i> Hooker f.	GAAN	Native	0.05		0.10			P	
<i>Galium aparine</i> L.	GAAP	Native	0.01	0.50	0.90	0.75	0.15	0.90	
<i>Geum magellanicum</i> Comm. ex Pers.	GEMA	Native	0.05	0.05				0.05	
<i>Gunnera magellanica</i> Lam.	GUMA	Native	0.65	0.20	P				
<i>Luzula alopecurus</i> Desv.	LUAL	Native		0.01	0.05		0.05		
<i>Macrachaenium gracile</i> Hooker f.	MAGR	Native		0.01					
<i>Marsippospermum grandiflorum</i> (L. f.) Hooker f.	MRGR	Native	P						
<i>Montia fontana</i> L.	MOFO	Exotic	0.01	0.01					
<i>Nothofagus antarctica</i> (Forster f.) Oersted	NOAN	Native	0.15		0.50				
<i>Nothofagus pumilio</i> (Poepp. et Endl.) Krasser	NOPU	Native	0.90	1.00		1.00	0.90	1.00	
<i>Osmorhiza depauperata</i> Phil.	OSDE	Native	0.45	0.90	0.95	0.90	1.00	1.00	
<i>Pernettya pumila</i> (L. f.) Hooker	PEPU	Native	0.40	0.20					
<i>Phleum alpinum</i> L.	PHAL	Native	0.30	0.20	0.60	0.15	0.01	0.30	
<i>Phleum pratense</i> L.	PHPR	Exotic		P					
<i>Poa pratensis</i> L.	POSP	Exotic	0.01	0.01	0.01	0.01		0.01	
<i>Poa</i> L. sp.	POPR	?	0.05	0.05	0.50	0.10		0.15	
<i>Ranunculus peduncularis</i> Sm.	RAPE	Native	0.01	0.01		P			
<i>Ribes magellanicum</i> Poiret	RIMA	Native	0.10	0.10	P			0.05	
<i>Rubus geoides</i> Sm.	RUGE	Native	0.15	0.15					
<i>Rumex acetosella</i> L.	RUAC	Exotic	0.01	0.01	0.01	P		0.01	
<i>Sagina procumbens</i> L.	SAPR	Exotic	0.00	0.10					
<i>Schizeilema ranunculus</i> (D'Urv.) Domin	SCRA	Native	0.80	0.75	0.80	0.01	0.01	0.40	
<i>Senecio magellanicus</i> Hooker & Arn.	SEMA	Native	0.01		0.10				
<i>Senecio smithii</i> DC.	SESM	Native	0.95	0.40					
<i>Stellaria media</i> (L.) Vill.	STME	Exotic	P						
<i>Taraxacum officinale</i> Weber	TAOF	Exotic	0.01	0.05	0.30	0.40	0.05	P	
<i>Trisetum spicatum</i> (L.) K. Richter	TRSP	Native		0.20	0.55	0.20	0.10	0.30	

Table 2 continued

Species	Code	N/E	Site types					
			W	S	ÑF	BLR	MHLF	LF
<i>Uncinia lechleriana</i> var. <i>lechleriana</i> Steudel	UNLE	Native	0.10	0.20	0.25	0.10	0.05	0.30
<i>Veronica serpyllifolia</i> L.	VESE	Exotic	0.15	0.10				
<i>Viola magellanica</i> Forster f.	VIMA	Native	0.15	0.60	P		P	0.65
Total species richness			41	40	28	23	18	28
Exotic species number			9	9	4	3	2	4

W = *N. pumilio*–*N. antarctica* forest wetland; S = Streamside *N. pumilio* forest; ÑF = *N. antarctica* forest; BLR = Edge between *N. pumilio* forest and grassland; MHLF = *N. pumilio* forest on a hillside; LF = *N. pumilio* forest on flat ground. ? Indicates unknown origin; P Indicates *not-sampled* species

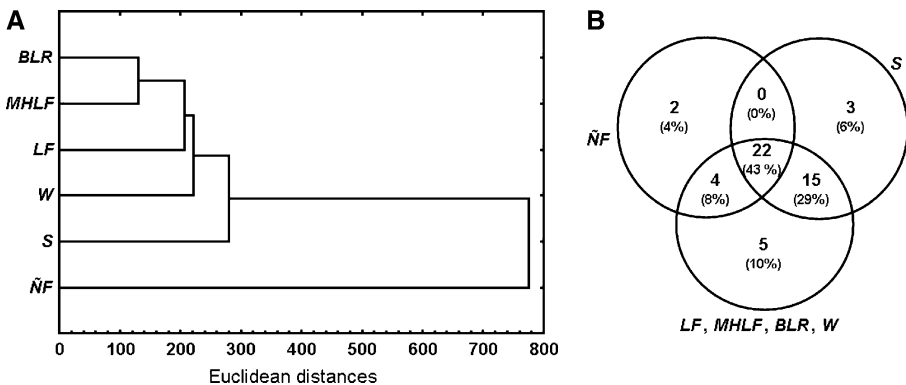


Fig. 2 Cluster analysis based in 38 understory species biomass data (A) and richness overlapping (B). MHLF = *N. pumilio* forest on a hillside, BLR = Edge between *N. pumilio* forest and grassland, LF = *N. pumilio* forest on flat ground, ÑF = *N. antarctica* forest, W = *N. pumilio*–*N. antarctica* forest wetland, S = Streamside *N. pumilio* forest

understory cover, as well as dicot and lower plants compared to the other site types. The least understory cover was found in MHLF and BLR (13%). Dicot and lower plants had a sparse cover in *N. pumilio* forests (MHLF, BLR and LF) with 9% and 4% respectively, and tree regeneration cover reached its maxima in S. Cover of bare floor and monocots presented interactions (Table 3) due to the different growing pattern in the wet site types. The bare floor proportion was higher in spring than summer, and maximum in BLR and MHLF. Monocot covers were higher in summer, and in ÑF and W.

Understory biomass varied with site types and seasons (Table 4). Dicot biomass was significantly higher in summer than in spring (85% higher). When site types were considered, all variables showed significant differences. Understory total biomass varied from 270 to 1420 kg ha⁻¹, with the maximum recorded in W and the minimum in MHLF. Tree regeneration biomass was higher in S, BLR and LF (up to 100 kg ha⁻¹) than other stands (less than 43 kg ha⁻¹). In S and W dicot biomass (300–600 kg ha⁻¹) and lower plant biomass (up to 330 kg ha⁻¹) were the greatest. Monocot biomass were maximum in ÑF (195 kg ha⁻¹) and reach the minimum in BLR and MHLF (less than 12 kg ha⁻¹).

For DCA analysis, only two ordination axes were retained for interpretation (eigenvalues of 0.754 for axis one and 0.553 for axis two). The major identified gradients for first axis were related with soil water availability, specific richness and biomass of dicots and lower plants, meanwhile second axis contrasted sites with different dominant tree species

Table 3 ANOVA results for mean forest floor cover (%) analyses, comparing six different site types and two seasons, in timber quality and associated non-timber quality stands of *Nothofagus* forests in Tierra del Fuego

Variables	Site types						Seasons				Site type × season interaction		
	W	S	NF	BLR	MHLF	LF	F test	Spring		Summer		F test	
Understorey cover	41.9d	36.0cd	30.4cd	15.4ab	11.2a	24.7bc	16.68**	18.1a	35.1b	51.09**	1.68 ns		
Debris cover	15.6a	16.9a	16.6a	19.1a	19.0a	25.4a	2.23 ns	17.1a	20.4a	2.90 ns	0.81 ns		
Bare floor cover	42.5a	47.1a	53.0a	65.5b	69.8b	49.9a	14.01**	64.8b	44.5a	74.5**	3.20*		
Regeneration cover	1.6a	7.1c	0.6a	4.3ab	1.7a	4.3ab	5.42**	2.7a	3.8a	1.72 ns	0.82 ns		
Dicot cover	22.9d	19.2cd	14.9bcd	8.4ab	5.0a	13.2abc	9.49**	8.5a	19.4b	39.58**	1.20 ns		
Monocot cover	7.6bc	4.0ab	12.0c	1.0a	0.2a	4.0ab	10.56**	3.0a	6.6b	11.04**	4.18**		
Lower plant cover	9.7c	5.8ab	2.8a	1.6a	4.2a	3.2a	6.01**	3.9a	5.3a	2.10 ns	1.57 ns		

W = *N. pumilio*-*N. antarctica* forest wetland; S = Streamside *N. pumilio* forest; NF = *N. antarctica* forest; BLR = Edge between *N. pumilio* forest and grassland; MHLF = *N. pumilio* forest on a hillside; LF = *N. pumilio* forest on flat ground. Significance levels of F test are indicated by: * $P < 0.05$; ** $P < 0.01$; ns = Not significant. Different letters within a same row represent significant differences at $P < 0.05$ by Tukey test

Table 4 ANOVA results for mean understory biomass (kg ha^{-1}) analyses, comparing six different site types and two seasons, in timber quality and associated non-timber quality stands of *Nothofagus* forests in Tierra del Fuego

Variables	Site types						Seasons			Site type \times season interaction	
	W	S	NF	BLR	MHLF	LF	F test	F test		F test	
								Spring	Summer		
Regeneration biomass	32.3abc	165.6d	42.2a	138.8cd	20.9ab	100.3bcd	7.96**	82.0a	84.7a	3.10 ns	0.38 ns
Dicot biomass	597.8d	297.8cd	138.5bc	60.1ab	32.7a	86.1abc	14.18**	141.9a	262.5b	21.25**	0.80 ns
Monocot biomass	74.1b	54.6b	195.5c	11.2a	0.8a	41.3b	23.94**	58.0a	67.9a	0.40 ns	1.37 ns
Lower plant biomass	714.9c	338.5bc	138.8a	99.4ab	232.1bc	247.5ab	7.68**	279.2a	311.2a	0.27 ns	0.87 ns
Total understory biomass	1419.2c	856.4bc	515.0ab	309.6a	268.5a	475.3a	13.45**	561.1a	762.2a	2.79 ns	0.60 ns

W = *N. pumilio*-*N. antarctica* forest wetland; S = Streamside *N. pumilio* forest; NF = *N. antarctica* forest; BLR = Edge between *N. pumilio* forest and grassland; MHLF = *N. pumilio* forest on a hillside; LF = *N. pumilio* forest on flat ground. Raw dates were transformed using the function $W = \ln(Y + 1)$, with Y = biomass. Significance levels of F test are indicated by: * $P < 0.05$; ** $P < 0.01$; ns = Not significant. Different letters within a same row represent significant differences at $P < 0.05$ by Tukey test

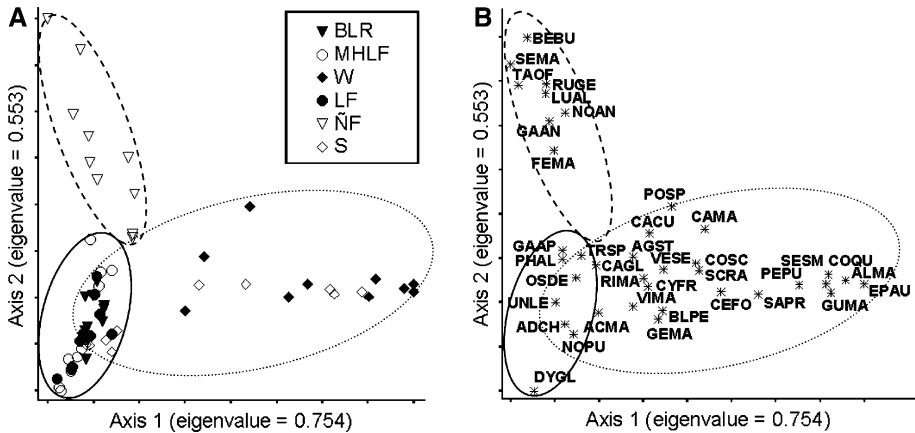


Fig. 3 DCA ordination for 60 plots (A) and 38 understory species (B) based on biomass data. LF = *N. pumilio* forest on flat ground, MHLF = *N. pumilio* forest on a hillside, BLR = Edge between *N. pumilio* forest and grassland, NF = *N. antarctica* forest, W = *N. pumilio*–*N. antarctica* forest wetland, S = Streamside *N. pumilio* forest. Species codes in Table 2. Circles enclose different site type plots according to the cluster analysis: dotted lines for *N. antarctica* forest (NF), entire line for *N. pumilio* forest (LF, MHLF and BLR), and dashed line for wet areas (W and S)

and monocots biomass. The three groups determined in the DCA analyses of plots (Fig. 3a) and plant species (Fig. 3b) were not totally coincident with the cluster analysis (Fig. 2a). In the DCA analysis, *N. antarctica* forest group included their regeneration, several xerophytes (e.g. *Senecio magellanicus*), one shrub (*Berberis buxifolia*) and one non-native (*Taraxacum officinale*) species. Wet forests included many hydrophilous plants (e.g. *Epilobium australe* and *Gunnera magellanica*), acidophilous vegetation (e.g. *Alopecurus magellanicus*), and palustrine species (e.g. *Senecio smithii*). In the last group, represented by *N. pumilio* forests, it was possible to find hydrophilous (e.g. *Dysopsis glechomoides*) and mesophilous species (e.g. *Adenocaulon chilense*).

Discussion

Ecological characterization of the site types

Forest ecosystems usually are constituted by several site types, determined by its biotic and abiotic characteristics. In *Nothofagus* forests, depth soil (Schlatter 1994), wind effect (Veblen 1979), altitude above sea level (Barrera et al. 2000) and resources availability rate (Schlatter 1994) are the most influential factors that determine forest structure. Sheltered valleys or mid-elevation hillside, with deep, good drained soils and high resource availability develop great tree biomass and marketable volume (Martínez Pastur et al. 1997), as LF and MHLF. However, habitat characteristics that improve forest tree growth do not necessarily favour understory development and richness, because microclimatic and edaphic conditions under overstory restrict vegetation growth (Reader and Bricker 1992; Martínez Pastur et al. 2002a). Among forest structure variables, stand density and overstory canopy cover influence understory diversity, because these determine light quality and quantity, and net precipitation that reach to the forest floor (Caldentey et al. 1998). Forest structures with large canopy cover only permit the development of sparse understory with little diversity of higher

plants (Reader and Bricker 1992), as in LF and MHLF. When altitude and water stress increase, as in MHLF, understory vegetation richness diminishes as well (Huston 1994).

Contrary, higher radiation reaches to the forest floor in stands with lower canopy cover (as in wetlands, streamside and *N. antarctica* forests), which increase understory diversity (Reader and Bricker 1992; Martínez Pastur et al. 2002a; Honnay et al. 2002a). In wet areas, woody plants develop jointly with a functionally and taxonomically diverse herbaceous level (Smith and Goodman 1986, 1987). Coexistence of several functional types permits more light use strategies, and increases richness too (Huston 1994). Periodic fluctuations of water table favour soil acidification and allow to the development of acidophilus species, as *Alopecurus magellanicus* and *Geum magellanicum* (Roig 1998). Edges between forest and grasslands are transitional ecosystems, where microclimate and soil conditions (Huston 1994) could allow better development of some xerophyte species (e.g. *Chilotrimum diffusum*), but not offer the necessary conditions for those species that need more overstory protection (e.g. *Adenocaulon chilense*). Finally, canopy cover variability allows microenvironment formation, which is usually found in *Nothofagus* forests (Ramírez et al. 1985; Martínez Pastur et al. 2002a).

Understory diversity in timber-quality forest and its associated non-timber-quality stands

Understory *Nothofagus* forest richness is scarce compared to other temperate woods around the world (Christensen and Emborg 1996; Liu et al. 1998; Wigley and Roberts 1997). Forest understory richness in Tierra del Fuego varied between 25 and 90 species (Moore 1983), which produce low diversity indexes. Richness is duplicated in similar latitudes of the boreal habitats of the Northern Hemisphere (Rothkugel 1916). This can be explained by the extreme climatic conditions during the growing season: a short growth period (Roig et al. 2002), low average temperatures, and low thermal amplitude between winter and summer (Ferreira et al. 1998; Grytnes et al. 1999; Odland and Birks 1999; Ohlemüller and Wilson 2000). Moreover, understory diversity patterns are related to overstory (Berger and Puettmann 2000), which are mainly mono-specific in Tierra del Fuego. Fuegian soils have low development (Rothkugel 1916), being unfavourable for many understory species. For this, most vegetation is widely adapted and distributed. The scarce shrub diversity observed could be attributed to low resources availability (Huston 1994), with few species able to tolerate competition with trees and herbs.

Exotic plant species in Tierra del Fuego arrived mainly from European meadows (Colantes and Anchorena 1993), and naturalize and grow freely in disturbed and undisturbed communities (Moore 1983) due to they have wide acclimatization ability. Intentional or accidental exotic plant introductions reduce beta diversity between site types, and compete with native vegetation for resources (Moore and Goodall 1977). Frequency of exotic species in the studied site types could be related to seed dispersal mechanisms, e.g. anemochore species (as *Taraxacum officinale*) are more frequent in windy stands (BLR and NF), and zoochore species (as *Cerastium fontanum*) are usual in wet areas, that are regularly used by several mammal and bird species (Lencinas et al. 2005).

Specific composition and spatial distribution of understory communities are related to biotic and abiotic environmental characteristics, and influence associated faunistic diversity (Fitter and Hay 1983; Robertson et al. 1988; Huston 1994). Associated non-timber-quality stands include all the understory plant species at forest landscape level, with a better representation of cover and biomass in comparison with timber-quality forests. Wet areas have the best comparative conservation value, because the high presence of rare plant species and functional groups, which are not present in the remainder site types. Huston (1994)

stated that plant diversity is directly related to soil water availability, and productivity is positively correlated with plant diversity, which could explain the higher proportion of exclusive species, cover and biomass in these wet areas. Likewise, tree species coexistence contributes to the maintenance of spatial heterogeneity in the forest soil resources utilization (Berger and Puettmann 2000), despite the adverse conditions for *N. pumilio*. This species can not tolerate water level fluctuations and could die in a short period of time (Roig 1998), while *N. antarctica* can tolerate flooding soils (Ramírez et al. 1985; Roig 1998) and live better in these marginal areas.

Contrary, timber-quality forests support a relatively low richness of understory plant species, and all of them could be found in associated non-timber-quality stands. Richness, floor cover and biomass under closed canopy cover are poor; therefore these stands have a reduced conservation value.

Forest management implications and mitigation alternatives

In this study, timber-quality forests occupy more than half of the landscape, with 23% of associated stands areas and 13% of non-forested surfaces (grasslands and peatlands). In forest regions of Norway non-timber-stands usually occupy 3–9% of the landscape, while 82–88% corresponds to timber-quality forests and 5–16% to bogs and lakes (Storaunet et al. 2005). Despite associated non-timber-quality stands occupy a small proportion of the landscape, there are intimately intermingled with timber-quality forests and have a great ecological importance due to numerous plant species only live there.

Silvicultural practices significantly affect forest structure of timber-quality stands, as well as its understory plant diversity (Martínez Pastur et al. 2000, 2002a; Gea et al. 2004). In southern Patagonia, harvesting was not carried out in associated non-timber-quality stands, but usually these are seriously affected during harvesting by road construction, worker camps or piling zones installation. In addition, *Nothofagus* wetlands and streamside forests are preferred by introduced beaver (*Castor canadensis*) for build dams, which modify this unique ecosystem (Martínez Pastur et al. 2006).

Forest management planning is carried out before the logging, but only includes timber-quality stands, and neglect the associated non-timber quality stands. On the other hand, theoretical proposed conservation strategies focus only on timber-quality forests (e.g. snag or hollow tree preservation) (Ojeda et al. 2007), leaving unprotected the characteristic vegetation of associated non-timber-quality stands. These stands must be included into the forest management planning and conservation strategies to reach a better conservation at landscape level. To be able to apply effective conservation measures, the following strategies need to be followed: (1) to include major studies about forest site types, area and conservation status of the associated non-timber-quality stands; (2) to determine the balance between areas that will be harvested and the associated non-timber-quality stands which will not be intervened; (3) to determine the ecology of understory species, especially the introduced ones and those negatively affected by forest management; and (4) to avoid human impacts over associated non-timber-quality stands.

When timber-quality stands gets into silvicultural practices, harvesting produce plant species losses during the first stages of the forest management (Martínez Pastur et al. 2002a). Associated non-timber-quality stands could act as understory vegetation reserves, due to they are spatially and intimately intermingled with timber-quality forests. After forest structure of timber-quality stands were recovered, associated non-timber-quality stands could act as sapling banks, due to their patch shape and spatial closeness with the impacted stands (Honnay et al. 2002b).

This kind of studies could help vegetation ecologists and land managers to understand the need for spatial heterogeneity among forest stands, to preserve seed bank reserves and animal habitats. Forest management should be modified and adapted according to the requirements of plant species impacted by forest harvesting. Fuegian forests have been traditionally managed through high grading cuttings or clear-cuts, and recently by shelterwood cuts (Schmidt and Urzúa 1982; Martínez Pastur et al. 1999a; Gea et al. 2004; Rosenfeld et al. 2006), which significantly affects the original diversity (plants, birds, insects and mammals) (Martínez Pastur et al. 1999b, 2002a; Pulido et al. 2000; Deferrari et al. 2001; Spagarino et al. 2001; Ducid et al. 2005). For this, a new silviculture regimen has been applied in Argentine Tierra del Fuego since 2000 (Martínez Pastur and Lencinas 2005; Martínez Pastur et al. 2005). It proposes to leave 30% of the timber quality forest area as aggregated retention and 20% basal area as dispersed retention (Martínez Pastur and Lencinas 2005; Martínez Pastur et al. 2007), which was defined to conserve the original biodiversity affected by forest management (Vergara and Schlatter 2006; Lencinas et al. 2007). Researches related to the implementation of different kinds of retention for improvement in conservation of harvested forest diversity should be accompanied with complementary studies about habitat fragmentation (Cornelius et al. 2000).

Conclusions

In *Nothofagus* forests in Tierra del Fuego, timber-quality stands support a relatively low richness of understory plant species, and all of them could be found in the associated non-timber-quality stands. Associated stands include numerous exclusive native and exotic species in variable frequencies, and sites with higher light and water availability have higher understory richness and biomass too, compared to closed canopy or drier stands. Consequently, these temperate timber-quality forests have a marginal value for understory plant species conservation. In the other hand, associated non-timber-quality stands could act as understory vegetation reserves for re-colonization of timber-quality forests when there are spatially and intimately intermingled. Dispersion of preserved species in associated stands could aid to recuperate lost species in timber impacted forest, e.g. by forest management, once the structure was recovered. Researches on associated non-timber-quality forests should be integrated within forest management planning, increasing their protection and minimizing the impacts inside them. These could improve plant species understory conservation at landscape and ecosystem level.

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