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## Forest Ecology and Management

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## Structural and environmental characterization of old-growth temperate rainforests of northern Chiloé Island, Chile: Regional and global relevance

Alvaro G. Gutiérrez<sup>a,b,\*</sup>, Juan J. Armesto<sup>b,c</sup>, Juan-Carlos Aravena<sup>d</sup>, Martín Carmona<sup>c</sup>, Natalia V. Carrasco<sup>e</sup>, Duncan A. Christie<sup>e</sup>, María-Paz Peña<sup>e</sup>, Cecilia Pérez<sup>c</sup>, Andreas Huth<sup>a</sup><sup>a</sup> Department of Ecological Modelling, Helmholtz Centre for Environmental Research (UFZ), Permoser Str. 15, 04318 Leipzig, Germany<sup>b</sup> Instituto de Ecología y Biodiversidad (IEB), Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile<sup>c</sup> Center for Advanced Studies in Ecology & Biodiversity (CASEB), Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Alameda 340, Santiago, Chile<sup>d</sup> Centro de Estudios Cuaternarios (CEQUA), Punta Arenas, Chile<sup>e</sup> Laboratorio de Dendrocronología, Facultad de Ciencias Forestales, Universidad Austral de Chile, Casilla 567, Valdivia, Chile

## ARTICLE INFO

## Article history:

Received 8 April 2008

Received in revised form 23 February 2009

Accepted 3 March 2009

## Keywords:

Old growth

Temperate rainforest

Forest structure

Constrained correspondence analysis

Stand age

Structural variability

## ABSTRACT

Old-growth forests are ecologically relevant reservoirs of biodiversity and provide valuable and unique ecosystem functions in the landscape. However, what constitutes an old-growth stand is confusing because the definition depends largely on the forest type under study. Despite the ecological importance of old-growth temperate rainforests in southern Chile in comparison to other global forests, no attempts have been made to characterize them as a way to assess their structural variability. Here, we characterized old-growth stands of Valdivian and North Patagonian rain forest types located in Chiloé Island (Chile, 42°30'S) using inventory data from 23 permanent plots (0.1 ha each) located in rural landscapes and protected areas of northern Chiloé Island. For each stand, its age (average age of the oldest trees present in each stand) and disturbance regimes (evidence of recent human impact, e.g. cuttings or fires, and tree growth rates) were used as defining old-growth criteria. We characterized the structure (tree species richness, size-density distributions, vertical stratification and presence of snags) and floristic composition of each stand. Environmental variables (i.e. temperature, distance to coastline and elevation) were related to stand structure using multivariate constrained correspondence analysis. Old-growth forests were commonly characterized by (a) tree basal areas >80 m<sup>2</sup>/ha; (b) density of shade-tolerant tree species in the emergent and dominant canopy layer >36%; (c) higher tree species richness (>7 tree species) than successional stands; (d) presence of large canopy emergents (>80 cm dbh, >25 m tall); (e) high vertical heterogeneity; and (f) minimum stand ages older than 200 years. Old-growth forests showed a distinctive structural variability and floristic diversity influenced both by stand age and disturbance history of the stands. Structural variability was also related to environmental differences among sites (e.g. air temperature, distance to coastline, soil types). Old-growth forest features described here can offer a baseline for managers interested in maintaining and restoring old-growth forest structure in southern temperate rain forests.

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## 1. Introduction

What constitutes an old-growth stand is usually confusing because there is no generally accepted or universally applicable definition (Hunter, 1989; Foster et al., 1996; Franklin and Van Pelt, 2004; Spies, 2004). In general, old-growth forests can be defined by low rates of human disturbance and the dominance of old

canopy trees (Hunter, 1989). Old-growth forests under this broad definition often have a complex structure and a heterogeneous spatial arrangement that varies depending on the forest type (Foster et al., 1996; Franklin and Van Pelt, 2004; Spies, 2004). There is a renewed interest in the unique structural and functional characteristics of old-growth forests because of their diminishing land cover, high relevance for the conservation of regional biodiversity and their value for global carbon storage (Harmon et al., 1990; Lindenmayer and Franklin, 2002; Van Pelt, 2007). As forests over vast areas of the world become logged and maintained in young successional stages (Laurance et al., 2006), unique services provided by old-growth ecosystems are increasingly imperilled.

\* Corresponding author at: Department of Ecological Modelling, Helmholtz Centre for Environmental Research (UFZ), Permoser Str. 15, 04318 Leipzig, Germany. Fax: +49 341 235 3500.

E-mail address: [bosqueciencia@gmail.com](mailto:bosqueciencia@gmail.com) (A.G. Gutiérrez).

Few areas of the world within the temperate zone still maintain old-growth forest ecosystems and only in the southern hemisphere such forests are dominated by broad-leaved, evergreen tree species. Among the last remnants of temperate old-growth rain forests in southern South America are significant areas along the coast of south-central Chile, 37–43°S (Smith-Ramírez, 2004). Interest in conservation of these last remnants of endemic-rich old-growth forests increased in recent years (Dinerstein et al., 1995; Armesto et al., 1998; Olson et al., 2001; Smith-Ramírez, 2004) because of growing threats due to logging, fire, the construction of new access roads into remote coastal areas (Smith-Ramírez, 2004), and expanding exotic forestry plantations (Armesto et al., in press), leading to fast rates of land-use change (Echeverría et al., 2007). In particular, in northern Chiloé Island (40–42°S), the progressive loss, fragmentation and subsequent degradation of forest cover is reducing the original biodiversity and ecological complexity (Echeverría et al., 2007; Jaña-Prado et al., 2007). Moreover, rapidly expanding eucalyptus plantations in northern Chiloé Island in the past decade are threatening the integrity of ecosystem functions in the rural landscape.

Knowledge of old-growth forest structure and function in temperate rainforests of South America remains sparse (but see Armesto et al., in press). As a consequence, limited conceptual and empirical understanding of old-growth forest functioning has been applied to policy decisions about land cover inventories, regional conservation of biodiversity and forest management. As in other parts of the world (Hendrickson, 2003), national forest inventories (e.g., CONAF-CONAMA-BIRF, 1999) have significant gaps in their ability to identify remnant old-growth stands. Consequently, proper identification and characterization of remnant old-growth rain forests is a key national priority for the long-term protection of forest-dwelling biological diversity (Armesto et al., 1998; Smith-Ramírez, 2004), the maintenance of carbon storage, and other relevant ecosystem services, such as hydrologic balance and soil nutrient cycling (Lara et al., 2003).

Despite the global importance of old-growth temperate rainforests in southern Chile because of their highly endemic and endangered biodiversity (Armesto et al., 1998) and unique nature of unpolluted biogeochemical cycles (Hedin et al., 1995), no attempts have been made to characterize them in terms of their structural variability and ecological values for regional conservation, ecosystem management and long-term ecological research. Here, we characterize old-growth forests of two major forest types in south-central Chile: Valdivian and North Patagonian temperate rainforests (Veblen et al., 1983; Armesto et al., 1996). The analysis is based on floristic, structural and environmental parameters shared by remnant forest stands found in protected and rural areas of northern Chiloé Island. Our main goal is to identify structural attributes that are most valuable for the biodiversity conservation and integrity of ecosystem services in these temperate rainforests. We also discuss the potential role of our characterization for regional conservation and management strategies. We specifically addressed the following questions relative to old-growth forest stands: (1) What structural features are common and unique to old-growth temperate rainforests in Chiloé Island?; (2) Is there a characteristically distinct tree species composition of old-growth Valdivian and North Patagonian temperate rainforests compared to younger forests of Chiloé Island?; (3) Is there a relationship between old-growth forest structure and local environment? These questions provide valuable information for policy decisions regarding improvement of national forest inventories and for enhancing the societal appreciation of the heritage represented by the last old-growth forests.

## 2. Material and methods

### 2.1. Study area

The predominant topography in northern Chiloé Island is low-elevation, rolling hills over highly organic postglacial soils (<1 m deep) or gentle sloping coastal mountains up to heights of

**Table 1**

Study site locations in northern Chiloé Island, Chile. Distance to coastline was estimated using GPS location and the orthogonal distance to the nearest coastline on the Pacific Ocean. Data sources: (1) this study; (2) Aravena et al. (2002); (3) Gutiérrez et al. (2008).

Study site	Plot name	Location	Elevation (m.a.s.l.)	Distance to coastline of Pacific Ocean	Reference
Abtao	MIXTO	42°22'S–74°02'W	540	7.2	(1)
Aguila	AGC	41°54'S–73°35'W	60	34.5	(2)
Ahuenco	AHUEN1	42°06'S–74°03'W	80	1.2	(1)
	AHUEN2		80		(1)
Caulin	CAULIN	41°50'S–73°36'W	26	30	(1)
Cole-Cole	COLE1	42°30'S–74°11'W	80	0.7	(1)
	COLE2		80		(1)
Guabun	GUAB1	41°46'S–74° W	130	1.2	(3)
	GUAB2		130		(3)
Koenig	KOENIG	41°58'S–73°35'W	74	36	(2)
Melleico	BRIGIDA	42°35'S–73°56'W	280	14.4	(1)
	ELI		280		(1)
	MELISA		280		(1)
	MELL1		200		(1)
	MILENA		280		(1)
	PILLO	145	(1)		
Quemado	QUEM1	41°51'S–73°36'W	40	34.3	(2)
Rapoport	RAP1	41°53'S–73°39'W	60	29	(2)
	RAP2		60		(2)
Senda Darwin	PAPIC	41°52'S–73°39'W	60	26.8	(2)
	SUCRE		60		(2)
	TEPU1		60		(2)
	TEPU2		60		(2)

**Table 2**

Climatic data from meteorological stations considered in the constrained correspondence analysis of forest stands in northern Chiloé Island (see Section 2).

	Meteorological station		
	Senda Darwin <sup>1</sup>	Punta Corona <sup>2</sup>	Castro <sup>3</sup>
Location	41°52'S–73°39'W	41°47'S–73°52'W	42°29'S–73°48'W
Elevation	60	56	24
Recording period	1996–2006	1911–2005	1950–2000
Yearly mean temperature	<i>T</i> (°C)	9.1	10.8
Yearly mean maximum temperature	<i>t</i> <sub>max</sub> (°C)	13.9	17.6
Yearly mean minimum temperature	<i>t</i> <sub>min</sub> (°C)	4.2	5.2
Annual rainfall	ppt (mm)	2157.8	1744.3
Summer rainfall (% of annual rainfall)		25	13
Winter mean temperature	JJA (°C)	8.1	8.5
Summer mean temperature	DJF (°C)	12.5	13

Data source: (1) Estación Biológica Senda Darwin; (2) Armada de Chile; (3) Dirección Meteorológica de Chile. JJA: June to August; DJF: December to February.

600 m (Table 1). In rural landscapes old-growth forest stands are part of a mosaic of bogs, remnant and secondary forest, shrublands, exotic plantations and artificial grasslands. The present rural landscape has been shaped by a recent history (less than 200 years) of widespread use of fire and logging to clear land for pastures and selective logging of many forest patches (Willson and Armesto, 1996; Torrejón et al., 2004). Prevailing climate is wet-temperate with strong oceanic influence (di Castri and Hajek, 1976). Rainfall, about 2000 mm annually, occurs all year round, but 13–25% falls during summer (January–March). The mean annual temperature is 9.1–10.8 °C. Mean monthly maximum temperature is 17.6 °C in coastal sites and 14.4 °C in inland sites (January). Minimum monthly temperature is 6.9 °C (coast) and 4.2 °C (inland, both in July) (Table 2).

## 2.2. Main forests types

Chiloé Island has a mixed composition of broad-leaved evergreen rain forests depending on topography, elevation and soils (Holdgate, 1961; Veblen et al., 1983; Armesto et al., 1996; Table 3). The North Patagonian forest type is found predominantly on relatively poorly drained flat areas, in the southern sector of the island, and at elevations above 400 m on the coastal range. This forest type is floristically defined by the dominance of shade-tolerant conifers (Podocarpaceae), in addition to *Drimys winteri* (Winteraceae) and *Nothofagus nitida* (Nothofagaceae) in the main canopy, together with *Tepualia stipularis* and other Myrtaceae tree species in the understory (Veblen et al., 1983; Donoso, 1993; Armesto et al., 1996). In contrast, Valdivian rain forests are largely concentrated in northern and low-elevation sites (below 400 m), slopes facing the Pacific Ocean, and well-drained soils. These forests are generally dominated by a different set of broad-leaved evergreen tree species, such as the canopy emergents *Eucryphia cordifolia* (Eucryphiaceae) and *Aextoxicon punctatum* (Aextoxicaceae), several Myrtaceae species in the main canopy and subcanopy and often lack *Nothofagus* spp. (Veblen et al., 1983; Donoso, 1993; Armesto et al., 1996). In both forest types, tree trunks and branches are profusely covered with epiphytic ferns (e.g. *Hymenophyllum* spp., *Hymenoglossum cruentum*, *Polypodium feullei*) and several species of flowering epiphytes and climbers (e.g. species of Gesneriaceae and Bromeliaceae), including the hemiepiphytic tree *Raukaua laetevirens* (Araliaceae). The presence of dense thickets of native *Chusquea* bamboos is important in large canopy openings formed by natural tree falls and in logged forests, where the canopy has been opened. Shrubs are uncommon, except along forest margins and on coastal cliffs.

## 2.3. Forest sampling

Forest stands sampled in northern Chiloé Island (Fig. 1), were selected on the bases of accessibility from nearby roads, land-

owners' willingness to grant access to their properties and visual attributes (e.g. tree sizes, stratification, logging or fire marks, trails) that allowed us to estimate age since last disturbance. We selected forest stands ( $n = 9$ ) that represented a successional chronosequence from 30 to 200 years as described by Aravena et al. (2002) and an additional group of stands, selected from rural and protected areas in northern Chiloé ( $N = 14$ ). The latter stands had an average canopy height of at least 12 m, and therefore are classified as mature forests by current national inventories (Fig. 1, CONAF-CONAMA-BIRF, 1999). Structural characteristics of these mature forests (e.g., presence of large emergent trees, a patchy canopy including tree-fall gaps, tree-size distribution, and absence of logging and fire) suggested an old-growth condition.

In each selected forest, we set up one to four 20 m × 50 m (0.1 ha) permanently marked plots for assessing forest structure and species composition. The number of plots per stand was mainly constrained by accessibility and forest patch size. Plots

**Table 3**

Tree species present in North Patagonian and Valdivian forest types in northern Chiloé Island, following Veblen et al. (1983) and the authors personal observations. Life-span is the mean estimated maximum longevity in Chiloé Island following (1) Veblen (1985); (2) Lusk (1996b); (3) Gutiérrez et al. (2008) and data from this study. Shade-tolerance according to Figueroa and Lusk (2001), Aravena et al. (2002), Donoso (2006) and personal observations.

Tree species	Family	Abbrev.	Life-span	Shade-tolerance
<b>North Patagonian forests</b>				
<i>Podocarpus nubigena</i>	Podocarpaceae	Pn	500 <sup>2</sup>	To
<i>Myrceugenia chrysocarpa</i>	Myrtaceae	Mc	nd	To
<i>Nothofagus nitida</i>	Nothofagaceae	Nn	193	I
<i>Saxegothaea conspicua</i>	Podocarpaceae	Sc	600 <sup>2</sup>	To
<i>Tepualia stipularis</i>	Myrtaceae	Ts	nd	Int
<b>Valdivian forests</b>				
<i>Aextoxicon punctatum</i>	Aextoxicaceae	Ap	349 <sup>3</sup>	To
<i>Amomyrtus meli</i>	Myrtaceae	Am	113 <sup>3</sup>	Int
<i>Dasyphyllum diacanthoides</i>	Asteraceae	Dd	nd	Int
<i>Luma apiculata</i>	Myrtaceae	La	nd	To
<i>Myrceugenia ovata</i>	Myrtaceae	Mo	nd	To
<i>Myrceugenia planipes</i>	Myrtaceae	Mpl	nd	To
<i>Rhaphithamnus spinosum</i>	Verbenaceae	Rs	nd	Int
<b>Shared species</b>				
<i>Amomyrtus luma</i>	Myrtaceae	Al	nd	To
<i>Caldcluvia paniculata</i>	Cunoniaceae	Cp	68	Int
<i>Crinodendron hookerianum</i>	Elaeocarpaceae	Ch	nd	Int
<i>Drimys winteri</i>	Winteraceae	Dw	250 <sup>1</sup>	I
<i>Eucryphia cordifolia</i>	Eucryphiaceae	Ec	329	I
<i>Gevuina avellana</i>	Proteaceae	Ga	82	Int
<i>Laureliopsis philippiana</i>	Monimiaceae	Lp	307	To
<i>Myrceugenia parviflora</i>	Myrtaceae	Mp	140	Int
<i>Raukaua laetevirens</i>	Araliaceae	Pl	nd	Int
<i>Weinmannia trichosperma</i>	Cunoniaceae	Wt	404	Int

nd: no data available; To: shade-tolerant, I: shade-intolerant, Int: intermediate tolerance; Abbrev.: abbreviation code according to the first letters of the binomial species name.

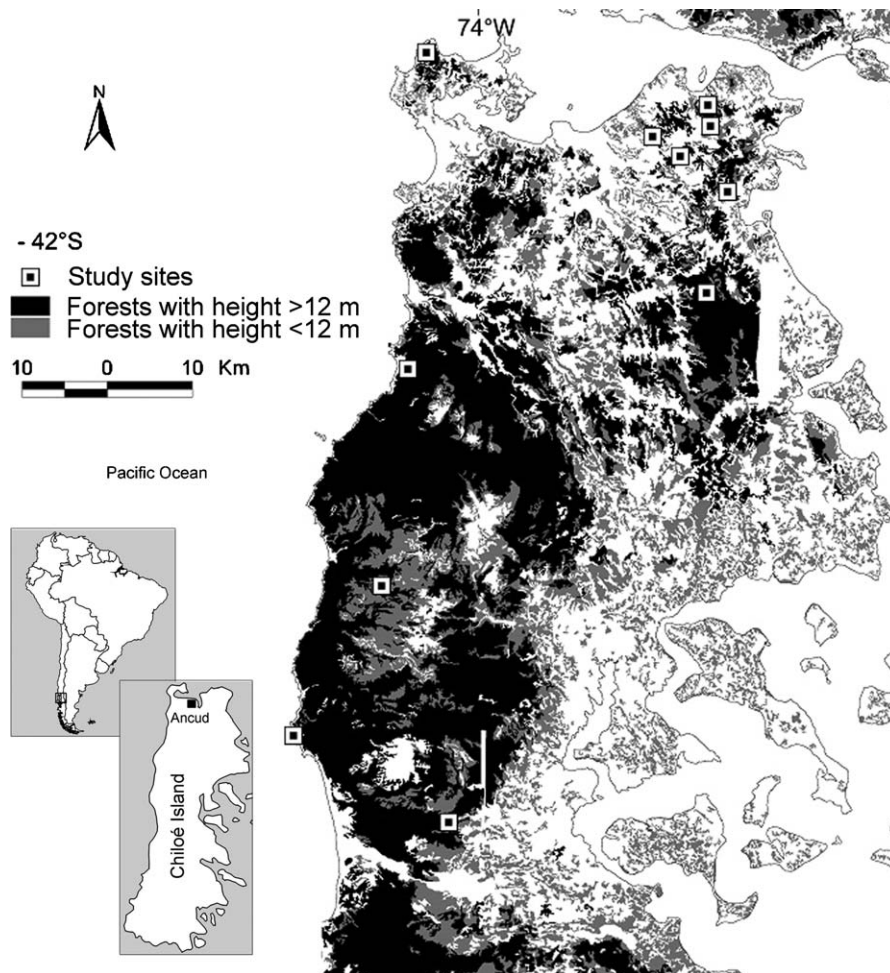


Fig. 1. Study site locations (squares) on northern Chiloé Island, Chile. Forest cover data from CONAF-CONAMA-BIRF (1999).

were set up between 1998 and 2005 and located at least 200 m away from edges with adjacent open areas. All trees rooted within each plot with stems  $>1.3$  m height and  $>5$  cm diameter at 1.3 m height (dbh) were permanently marked with numbered aluminium tags, identified to species, and their dbh measured to the nearest cm. Canopy classes for each tree were recorded as: (1) emergent, above canopy height; (2) dominant, in the canopy tier; (3) subcanopy, directly under the canopy with light only from above; and (4) understory, permanently shaded. Additionally, each tree was classified as (1) alive (healthy); (2) some branches dead; or (3) standing dead (snags).

Increment cores were obtained from a sample of  $>10$  of the largest trees in each stand to estimate the minimum stand age. Tree cores were processed following standard dendrochronological techniques (Stokes and Smiley, 1968) and tree ages were assessed by counting annual growth rings. When mean age of the 10 oldest trees was  $<100$  years, we classified the stand as young forests, representing the building phase of stand development, and mean age of all trees provided a suitable estimate of stand age (Aravena et al., 2002). When the mean age of the 10 oldest trees was  $>100$  years, the stand was classified as mature. In the latter case, we considered the mean age of the 10 oldest trees as an estimate of stand age. Using the mean of all cored trees would underestimate the stand age for mature forests because of their skewed age distributions due to the numerous presence of juvenile trees (Aravena et al., 2002). For young stands, the age of the 10 oldest trees would overestimate stand age because of the presence of few remnant old trees (Aravena et al., 2002).

We characterized stand structure in terms of tree species richness, size (dbh) distribution, canopy heterogeneity (number of tiers) and frequency of snags. To provide a quantitative basis for comparing dbh distributions (trees  $>5$  cm dbh) among plots, we fitted Weibull functions to the dbh frequency distribution of all trees in each plot (Bailey and Dell, 1973). Probability density distributions were fitted to each diameter distribution using a maximum-likelihood algorithm (Cohen, 1965). Weibull distributions can accommodate a wide variety of shapes as indicated by the shape parameter “ $c$ ”. When  $c = 1$ , dbh distribution fits a negative exponential, when  $c > 1$ , the function is unimodal, either positively skewed ( $1 < c < 3.6$ ), normal ( $c = 3.6$ ), or negatively skewed ( $c > 3.6$ ) (Bailey and Dell, 1973).

#### 2.4. Old-growth criteria

The old-growth condition was defined by the assessment of stand age and the evidence of disturbance in each stand (Hunter, 1989; Foster et al., 1996). Stand ages were used to determine whether dominant canopy trees reached their average life expectancy. In Chiloé, life spans of conifer tree species (Podocarpaceae) can be  $>500$  years whereas most angiosperms have average life spans of about 300 years (Table 3). Following Lorimer et al. (2001), estimated stand ages representing at least one-half of the estimated life span of the main canopy tree species were considered indicators of old-growth condition. Because extensive land-use change in Chiloé Island dates back only to the late 19th and early 20th century (Willson and Armesto, 1996; Torrejón et al.,

2004), a stand age >150 years strongly suggest that the stand has remained largely unaffected by direct human impact over the past two centuries. We further evaluated the undisturbed condition of mature forest stands (Hunter, 1989) by searching for stumps from selective logging and scars from human-set fires. Only stands without evidence of disturbance were considered old-growth.

A heterogeneous canopy structure is also a relevant attribute characterizing old-growth forests (Spies and Franklin, 1991). Based on the canopy classes defined above, we assessed the heterogeneity of vertical canopy structure using the Berger-Parker diversity index  $d$  (Magurran, 2004). This index provides a measure of stratification and canopy heterogeneity through the proportional importance of the most abundant canopy class:  $1/d = 1/(N_{\max}/N)$ , where  $N_{\max}$  is the number of individuals in the canopy class with the highest number of individuals and  $N$  is the total number of individuals in the stand. A high value of this index would reflect greater vertical heterogeneity, which is often associated with the old-growth status (Aber, 1979; Spies and Franklin, 1991).

Tree basal area, density, the  $c$  parameter of dbh distributions, dbh range, the number of canopy tiers, presence of snags, and tree species richness per plot were parameters used to characterize old-growth stands, previously defined by using the above criteria. In addition, the presence of shade-tolerant tree species in the dominant canopy layers (emergent and dominant) was used as an indicator of advanced successional age (Oliver and Larson, 1990). Linear regressions between each structural characteristic and stand age were used to assess the change of old-growth structural attributes through the advanced stages of stand development.

## 2.5. Multivariate analysis

We conducted floristic analyses for all plots sampled ( $N = 23$ ) and then separately for those plots identified as old growth by the

criteria specified above ( $N = 11$ , Table 4). Cluster analyses based on tree species presence (dbh >5 cm) in stand inventories were used to define species associations. Cluster analyses were based on Jaccard distances using the unweighted pairing with arithmetic mean (UPGMA) as the linkage method (Kaufman and Rousseeuw, 1990). The groups defined by clustering were tested using the Partitioning Around Medoids (PAM) method, with the number of clusters determined by maximizing the average silhouette (Kaufman and Rousseeuw, 1990).

Multivariate analysis was used to relate differences in tree species composition and forest structure to environmental factors and stand age. We carried out a gradient analysis using a Constrained Correspondence Analysis (CCA, a.k.a. canonical correspondence analysis) (Ter Braak, 1986) as a direct ordination method to relate environmental variables to basal area and density of tree species per plot. Environmental variables considered in the CCA were elevation, distance to the coastline (estimated using the plot GPS location and the orthogonal distance to the nearest coastline of the Pacific Ocean) and climatic variables for each sampled stand (Table 2). CCA is robust and usually preferable to other ordination methods (i.e. Detrended Correspondence Analysis). Some advantages of CCA are its good performance with highly inter-correlated environmental variables, and with situations where some factors determining tree species composition are unknown (Palmer, 1993). CCA calculates the proportion of the variation explained by each axis, the correlation between each canonical axis and each species axis, and the variation of species composition explained by the stand variables. The correlation between each variable and the canonical axes provides insights into factors that influence vegetation structure. According to Legendre and Legendre (1998), rare species that have little influence on vegetation structure may cause ordinations to be artificially aligned. Therefore, we removed from the analysis those species only found in one site. We performed Monte Carlo permutation tests ( $n = 10,000$ ) (Legendre and Legendre, 1998) to

**Table 4**  
Plot classification according to old-growth criteria discussed in this study for forests of northern Chiloé Island (see Section 2).

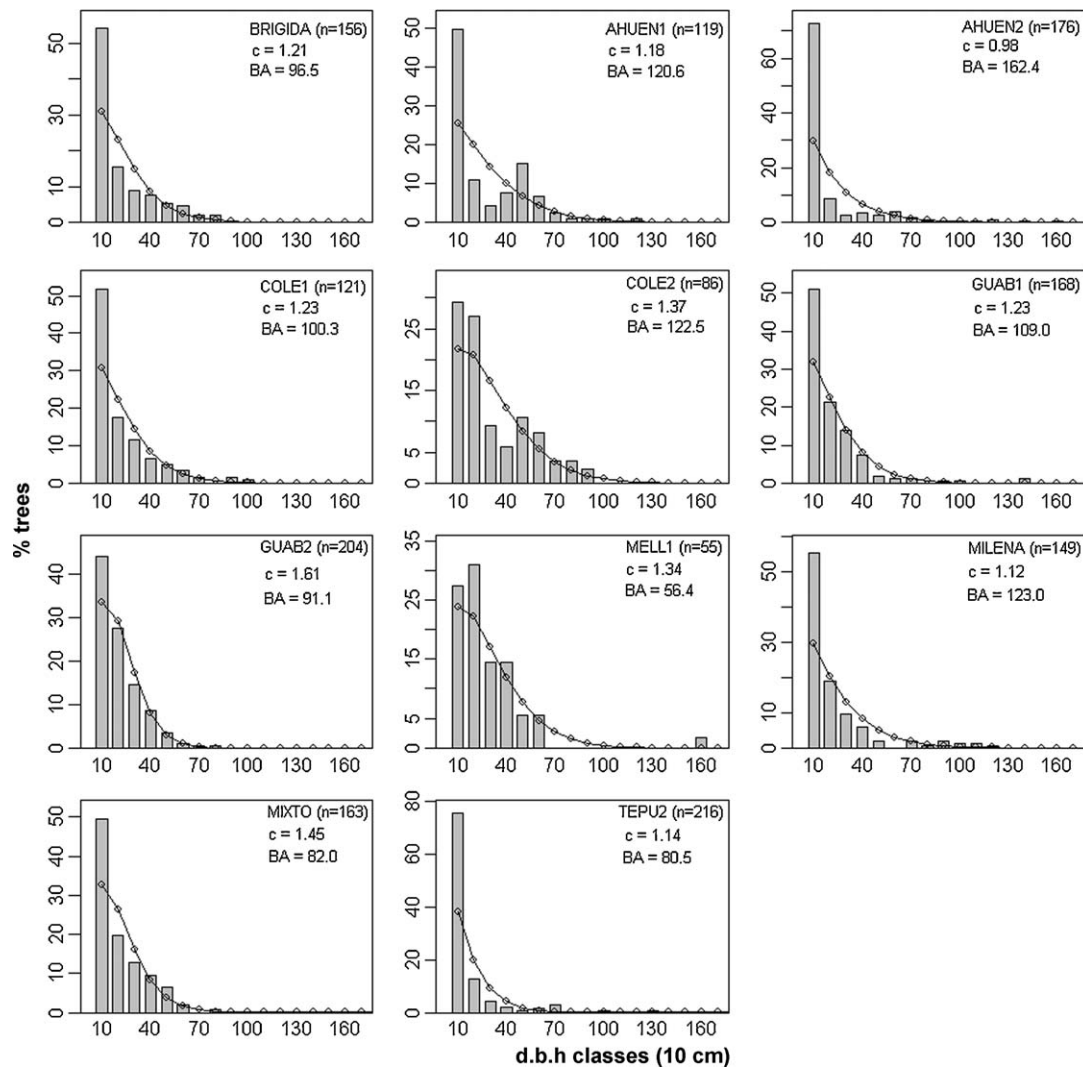
Plot name	N	Basal area (m <sup>2</sup> /ha)	Tree ages (years)			Stand-age	%Shade-tolerants	Evidence of human impact	Classification
			Mean	10 oldest	The oldest (species <sup>a</sup> )				
QUEM1	39	72.9	88.8	175.7	404 (Wt)	2 <sup>b</sup>	0.0	Fire	Young
PAPIC	10	22.0	11.2	11.2	14 (Dw)	11	0.0	Fire	Young
RAP2	30	44.8	33.3	40.2	46 (Dw)	33	1.4	Fire	Young
CAULIN	65	98.3	42.3	85.4	118 (Pn)	42	37.9	Selective cuttings	Young
PILLO	10	107.0	47.6	47.6	68 (Dw)	47	84.1	Selective cuttings	Young
RAP1	38	16.7	49.3	104.8	329 (Ec)	49	0.0	Fire	Young
SUCRE	31	60.2	61.5	111.7	200 (Pn)	112	16.2	Fire	Mature
MELISA	10	102.8	112.7	112.7	157 (Lp)	113	96.2	None	Mature
ELI	11	109.9	119.0	127.2	211 (Lp)	127	92.2	None	Mature
TEPU1	40	71.9	67.2	129.1	174 (Lp)	129	25.5	None	Mature
AGC	37	105.3	79.8	132.7	234 (Ec)	133	2.2	Selective cuttings	Mature
KOENIG	39	137.6	68.9	134.0	336 (Sc)	134	30.6	Selective cuttings	Mature
BRIGIDA <sup>c</sup>	4	96.5	172.8	–	192 (Lp)	173	97.0	None	Old-growth
MILENA	12	123.0	166.7	189.1	239 (Lp)	189	100.0	None	Old-growth
TEPU2	40	80.5	96.0	204.6	311 (Sc)	205	41.7	None	Old-growth
MELL1	48	56.4	123.8	217.1	307 (Lp)	217	84.0	None	Old-growth
AHUEN2	30	162.4	153.9	242.7	308 (Ec)	243	76.9	None	Old-growth
COLE1 <sup>c</sup>	–	100.3	–	–	–	250	97.6	None	Old-growth
COLE2 <sup>c</sup>	–	122.5	–	–	–	250	100.0	None	Old-growth
GUAB2	29	91.1	168.4	276.9	325 (Ap)	277	97.6	None	Old-growth
GUAB1	31	109.0	171.1	282.9	349 (Ap)	283	81.1	None	Old-growth
AHUEN1	49	120.6	160.4	283.2	297 (Ec)	283	92.3	None	Old-growth
MIXTO	20	82.0	202.0	308.6	399 (Pn)	309	36.2	None	Old-growth

N: number of cored trees. Mean age represents the average of all trees cored. %Shade-tolerants is the percentage of shade-tolerant trees in the dominant and emergent canopy layers.

<sup>a</sup> Represents the species of the oldest tree found in the plot.

<sup>b</sup> Known age since the last stand-devastating anthropogenic fire to the time of plot sampling.

<sup>c</sup> Limited or no age data were obtained because of high wood density of main canopy species. Mature: stand age >100 years but not fulfilling the structural criteria for old-growth.



**Fig. 2.** Tree-size structure (trees >5 cm dbh) in old-growth forest plots on northern Chiloé Island. Lines indicate the Weibull function fitted to each size distribution.  $N$  = number of trees;  $BA$  = total basal area ( $m^2/ha$ );  $c$  = shape parameter  $c$  of the Weibull distribution. Note different scale on the y-axis.

assess whether the observed patterns differed from random. Statistical analyses were conducted in R statistical environment (R-Development-Core-Team, 2005). Species nomenclature follows Marticorena and Quezada (1985) and Mabblerley (1997).

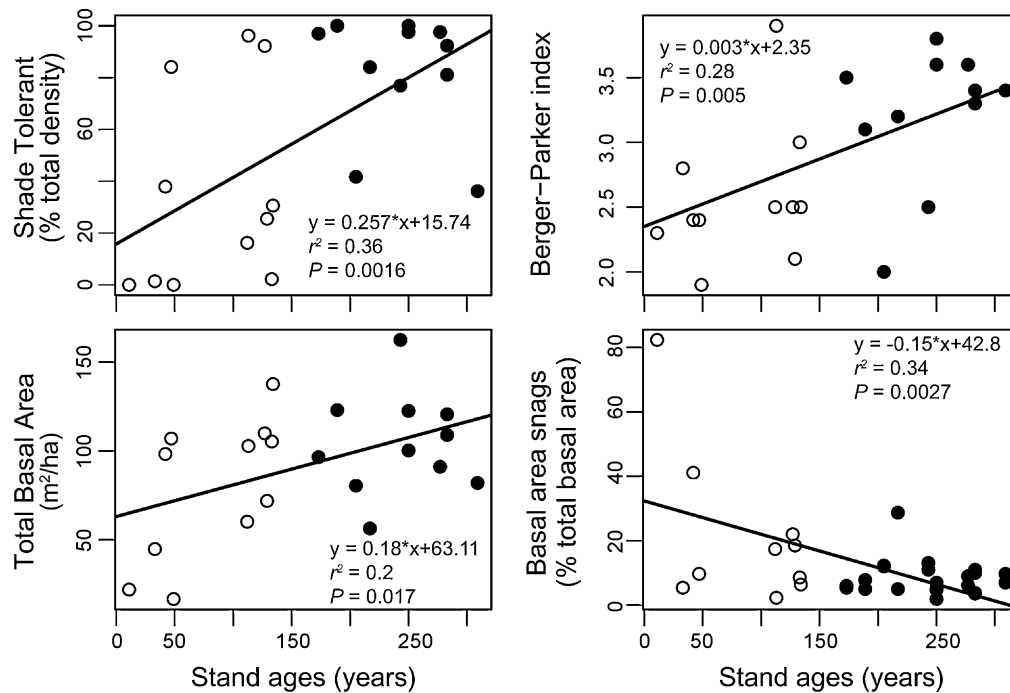
### 3. Results

#### 3.1. Old-growth forest structure

From the 23 plots sampled, 11 fitted the multiple criteria used to define old-growth status (Table 4). Mean minimum ages of the 10 oldest trees in these 11 stands were >189 years, with maximum values >239 years (Table 4). These results suggest that estimated stand ages of >150 years are good indicators of old-growth condition, as most canopy trees have reached their average life expectancy. These 11 stands represented forests without evidence of human disturbance through logging or fire. Although no tree age data were available for COLE1 and COLE2 plots, they were also classified as old-growth stands because their density, basal area and dbh distributions strongly suggested an uneven age structure (Fig. 2). Moreover, these stands are found within a remote and unbroken forest sector of Chiloé National Park, without human occupation or transit and had significant presence of shade-tolerant tree species in emergent and dominant canopy tiers (>97%

of emergent and canopy tree densities). This canopy structure suggests that the first cohort of pioneers had disappeared and the stand taken over by mid and late-successional tree species, a process that would take about three hundred years. Shade-tolerant species accounted for 36–100% of emergent and canopy dominant tree densities in all old-growth stands inventoried (Table 4) and the proportion of shade-tolerant tree species in the canopy increased linearly with stand age ( $r^2 = 0.37$ ,  $P < 0.005$ ,  $n = 23$ , Fig. 3).

Tree species richness in the canopy of 11 plots classified as old-growth ranged from 5 to 12 (mode = 7 tree species in 0.1 ha). Despite some exceptions (AHUEN2, TEPU2), Berger-Parker index was usually high in old-growth plots (median = 3.4, Table 5, Appendix A) and its value increased linearly with increasing stand age ( $r^2 = 0.28$ ,  $P = 0.005$ ,  $n = 23$ , Fig. 3). Tree-size (dbh) distributions for the 11 old-growth plots had  $c$  parameters ranging from 0.98 to 1.6, representing steeply descending, negative exponential, and unimodal (positively skewed) dbh distributions (Fig. 2). Tree densities (>5 cm dbh) of old-growth forest plots ranged from 1075 to 2160 individuals per hectare. Total tree basal area (Fig. 3) increased linearly with increasing stand age ( $r^2 = 0.20$ ,  $P < 0.05$ ,  $n = 23$ , Fig. 3). Particularly one site, MELL1 had a low basal area and tree density because of the large area of tree-fall gaps in the stand (ca. 50% of plot area). Excluding MELL1, basal area of old growth



**Fig. 3.** Structural attributes of forest stands related to their estimated stand ages. Filled circles represent old-growth stands; open circles indicate non old-growth stands based on evidences of disturbance.

stands ranged from 80.5 to 162 m<sup>2</sup>/ha (including snags). Large old trees (>80 cm dbh), occupying the emergent tree layer, represented up to 5.8% of total stem density. Snags represented at least 29% of stem density and 28% of total basal area in all old-growth stands and their abundance decreased linearly with stand age ( $r^2 = 0.34$ ,  $P < 0.005$ ,  $n = 23$ , Fig. 3). Mean quadratic dbh of snags ranged from 16.7 to 54.9 cm (Table 5).

### 3.2. Floristic composition

The distinction of floristic groups was similar between all plots surveyed and plots classified as old-growth (Fig. 4). These main floristic groups identified were rather consistent with the distinction of Veblen et al. (1983, see also Armesto et al., 1996) between North Patagonian (Groups B and C; Fig. 4a and b) and Valdivian coastal rain forests (Groups A, D and E; Fig. 4a and b). PAM component analyses showed that plot clusters accounted for 38.6% (all forest plots) and 46.9% (old-growth plots only) of the

variation in floristic composition, whereas species clusters accounted for 24.4% (all forest plots) and 35.1% (old-growth plots analysis) of the point variability.

Plots belonging to Valdivian rain forests (Fig. 4a and b) were characterized by tree species, such as *A. punctatum*, *Luma apiculata*, *Myrceugenia ovata*, *Myrceugenia planipes* and *Rhaphitamnus spinosus*, which are absent from North Patagonian forest plots. In contrast, the group of plots belonging to North Patagonian rain forests (Fig. 4a and b) were characterized by the presence of the conifer *Saxegothaea conspicua* which is absent from groups A, D and E (Fig. 4a and b). Some species such as the understory shrub *Crinodendron hookerianum*, the canopy trees *N. nitida*, *Podocarpus nubigena* and *T. stipularis* were always present in plots of groups II and III (i.e. North Patagonian rain forest) but were occasionally present in groups I and IV (i.e. Valdivian rain forest) (Fig. 4). *Amomyrtus luma*, *D. winteri*, *Caldcluvia paniculata*, *Laureliopsis philippiana* and *Weinmannia trichosperma* were shared between both plot groups. *Myrceugenia chrysocarpa* was only present in the understory of old-growth North Patagonian forest plots, whereas *Dasyphyllum diacanthoides* was represented only in old-growth Valdivian rain forests. *Amomyrtus meli* was also absent from old-growth North Patagonian forests.

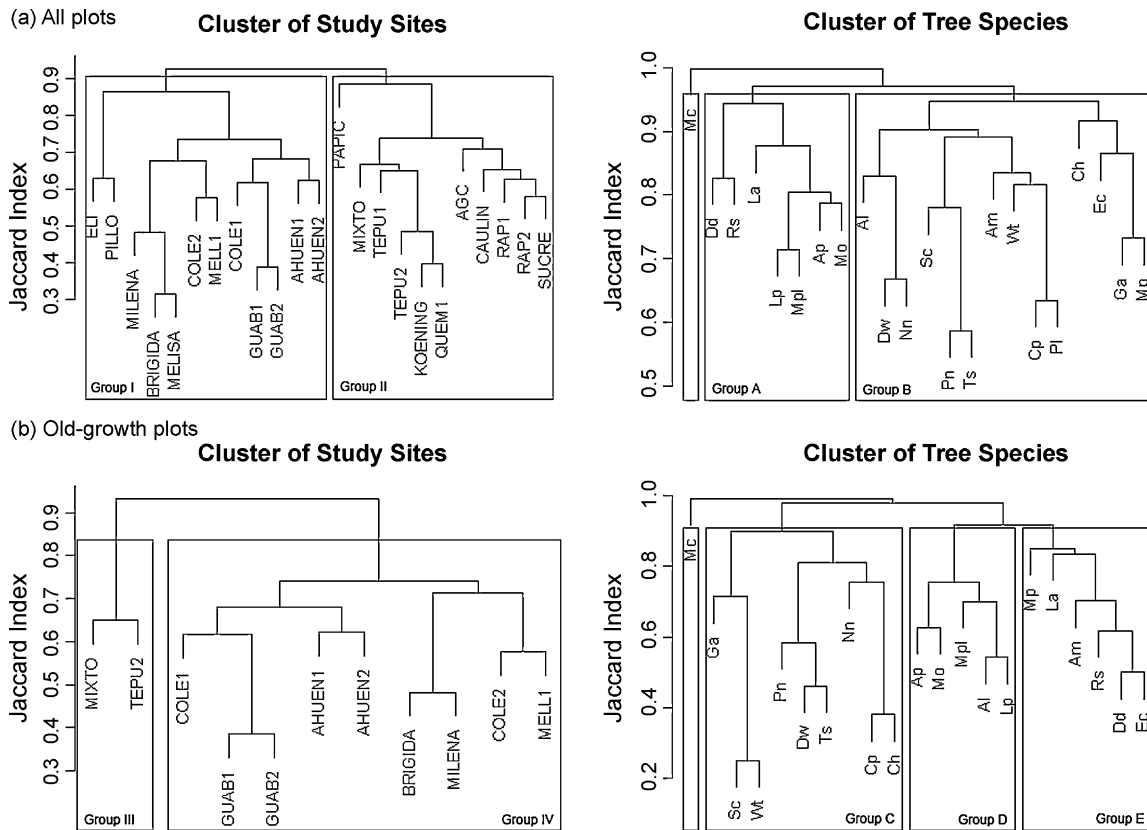
Based on the floristic classification of forest types described above, we averaged the density and basal area of old-growth stands belonging to Group III (North Patagonian rain forest type,  $n = 2$ ), and old-growth stands belonging to Group IV (Valdivian rain forest type,  $n = 9$ ) (Table 6). North Patagonian old-growth forests were numerically dominated by the understory tree species *T. stipularis*, the main canopy shade-tolerant conifer *P. nubigena* (shade-tolerant) and by the semi-tolerant *D. winteri*. Valdivian old-growth forests were numerically dominated by shade-tolerant tree species such as *A. luma*, *M. ovata* and *L. philippiana*. Density of all Myrtaceae tree species pooled represented the 59% of stem density in old-growth Valdivian rain forests, whereas in North Patagonian plots it was only 33%. Basal area of old-growth North Patagonian rain forests was largely accounted by canopy emergents such as *N. nitida* (shade-intolerant), *P. nubigena* and *D. winteri*. In Valdivian old-growth forests, basal area was dominated by shade-tolerant tree species such as *L. philippiana*, *A. punctatum* and *A. luma*. The large emergent,

**Table 5**

Range of structural attributes (median value in parenthesis, stems >5 cm dbh) in old-growth forest stands of northern Chiloé Island. MQD: mean quadratic diameter.

Stand variables	
Estimated stand age (years)	173–309 (242)
Basal area <sup>a</sup> (m <sup>2</sup> /ha)	80.5–162 (104.7)
Density <sup>a</sup> (N/ha)	1075–2160 (1513)
Canopy composition	
Tree species (species)	5–12 (7)
Berger-Parker index (–)	2.0–3.8 (3.4)
Shade-tolerant tree species (% trees in emergent and dominant canopy layer)	36–100 (92.3)
dbh structure	
Shape parameter <i>c</i> of the Weibull distribution (–)	0.98–1.6 (1.2)
% of trees dbh > 80 cm (% of total stem density)	0–5.4 (2.4)
Snags	
MQD (cm)	16.7–54.9 (30.8)
Density (%)	3.2–29.1 (5.8)
Basal area (%)	2–28 (6.1)

<sup>a</sup> Excluding MELL1 because it has 50% of plot area in canopy gap.



**Fig. 4.** Cluster analysis of floristic compositions of sites and tree species associations (>5 cm dbh) for (a) all plots and (b) old-growth plots sampled in temperate rainforests of northern Chiloé Island. Dendrogram was based on Jaccard's distance calculated from tree species densities (stems >5 cm dbh) using UPGMA as the linkage method. Boxes represent clusters determined after testing the groups detected using the Partitioning Around Medoids method, with the number of clusters determined by maximizing average silhouette (Kaufman and Rousseeuw, 1990).

shade intolerant tree species *E. cordifolia* (Table 3), was rarely present in old-growth North Patagonian forests, while having low density and basal area in old-growth Valdivian forests sampled (Table 6). North Patagonian forests were characterized by lower presence of shade-tolerant tree species in the main canopy (Table 4).

### 3.3. Forest structure and the environmental gradient

Examination of the constraining variables (Fig. 5a and b; Table 7) showed that there are two main gradients associated with major changes in tree species density and basal area in the studied forest

**Table 6**

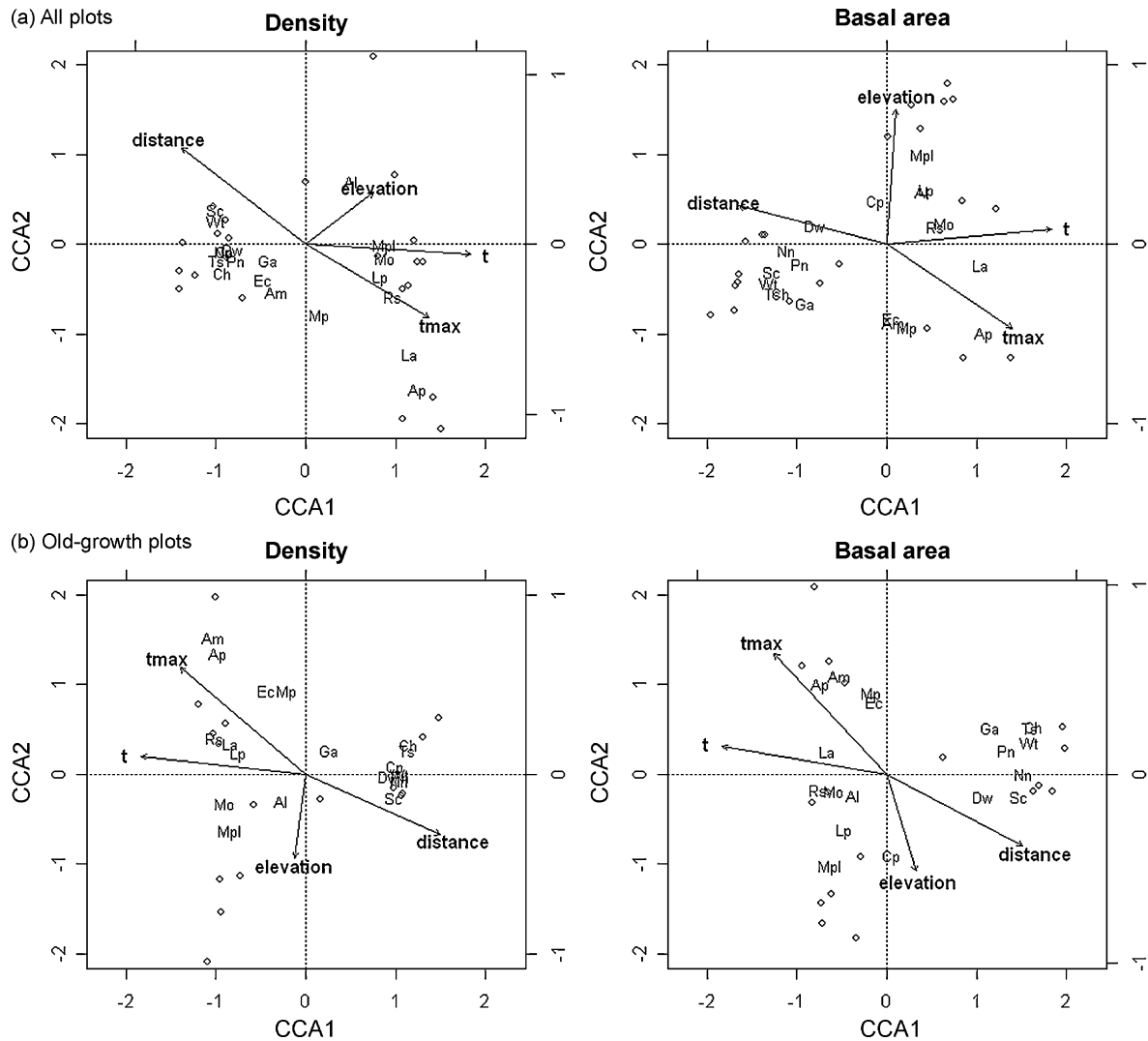
Mean density of trees (stems >5 cm dbh, N/ha) and mean basal area (m<sup>2</sup>/ha ± standard error) of main canopy tree species in old-growth stands of northern Chiloé Island.

Tree species	North Patagonian (N = 2)		Valdivian (N = 9)	
	Density	Basal area	Density	Basal area
<i>A. punctatum</i>	a	a	126 ± 53	21.6 ± 10.3
<i>A. meli</i>	a	a	28 ± 12	1.2 ± 0.7
<i>L. apiculata</i>	a	a	73 ± 31	9.3 ± 5.9
<i>M. ovata</i>	a	a	207 ± 107	3.4 ± 1.4
<i>M. planipes</i>	a	a	283 ± 85	7.5 ± 2.9
<i>R. spinosum</i>	a	a	17 ± 8	0.1 ± 0.1
<i>M. chrysocarpa</i>	10 ± 10	0.03 ± 0.03	a	a
<i>W. trichosperma</i>	17 ± 12	9.2 ± 6.3	0 ± 0	0 ± 0
<i>S. conspicua</i>	23 ± 12	1.4 ± 1.3	a	a
<i>N. nitida</i>	167 ± 38	20.2 ± 6.1	0 ± 0	0 ± 0
<i>C. hookerianum</i>	97 ± 49	0.4 ± 0.2	0 ± 0	0 ± 0
<i>P. nubigena</i>	517 ± 80	15.8 ± 3.1	1 ± 1	0.7 ± 0.7
<i>T. stipularis</i>	620 ± 376	7.5 ± 4.5	1 ± 1	0.04 ± 0.04
<i>M. parviflora</i>	7 ± 7	0.02 ± 0.02	19 ± 18	0.2 ± 0.2
<i>D. winteri</i>	367 ± 116	12.4 ± 7.4	27 ± 17	2.3 ± 1.4
<i>A. luma</i>	117 ± 29	1.1 ± 0.5	375 ± 154	13.1 ± 2.8
<i>L. philippiana</i>	40 ± 26	1.4 ± 0.8	380 ± 51	32.6 ± 7.0
<i>G. avellana</i>	10 ± 10	1.4 ± 1.4	6 ± 5	0.1 ± 0.1
<i>C. paniculata</i>	217 ± 148	1.4 ± 1.0	6 ± 5	2.2 ± 1.9
<i>E. cordifolia</i>	0 ± 0	0 ± 0	9 ± 6	9.8 ± 6.1
Others <sup>b</sup>	3 ± 3	0.01 ± 0.01	41 ± 41	0.4 ± 0.4

<sup>a</sup> Absent in the forest type.

<sup>b</sup> *D. diacanthoides* and *R. laetevirens*.





**Fig. 5.** Canonical correspondence analysis ordination diagrams (biplots) of basal area and density for (a) all forest plots and (b) old-growth forest plots. Sites are represented by circles, species are represented by their name abbreviations from Table 3. The proximity between species indicates occurrence in similar environments. Constrained variables are represented by arrows, which point toward increasing values of that variable and extend in both directions. The arrow relative length is directly proportional to the importance of the variable in influencing community structure. A smaller angle between the arrow and the constrained ordination axis indicates greater relationship of the variable to the derived CCA gradient. Distance: distance to the nearest coastline.

stands: one of decreasing temperatures with distance from the coast (first constrained axis, CCA1) and one of decreasing temperature with altitude (second constrained axis, CCA2). In both analyses (all plots and old-growth plots), the best environmental predictors were mean air temperature, mean maximum temperature and distance to the coastline for CCA1; and elevation and mean maximum temperature for CCA2 (Fig. 5a and b; Table 7). Other variables (Table 2) were discarded because they were collinear (redundant). The amount of the total variation in both basal area and density explained by environmental parameters was >41% and significant in both analyses (Monte Carlo permutations,  $P < 0.005$ ).

#### 4. Discussion

##### 4.1. Structural attributes and heterogeneity of old-growth southern forests

Our results confirm that many remnant forests in the rural mosaic of Chiloé Island and forests protected in private and public parks, without evidence of human disturbance (such as selective logging or fire scars), with a complex vertical profile, and having stand ages >200 years old can be defined as old

growth. Old-growth stands in northern Chiloé Island are also characterized by (a) tree basal areas of at least 80 m<sup>2</sup>/ha; (b) density of shade-tolerant tree species in the emergent and dominant canopy layer >36%; (c) seven or more tree species represented in the main canopy; (d) presence of large, often emergent, trees (>80 cm dbh); and (e) a high vertical heterogeneity indicated by a high value of Berger-Parker index. These stand attributes are consistent with other old-growth stand descriptions in Chiloé and in the mainland (Table 8). We propose to use these structural attributes in future forest inventories for the recognition of the old-growth condition and for mapping old-growth evergreen, broadleaved temperate rainforests in Chile. Tree species richness, densities and basal areas of old-growth forest stands in Chiloé Island are also comparable to old-growth forests elsewhere in the temperate region (Table 8). From these comparisons, old-growth forests of Chiloé Island had lower basal areas than old-growth evergreen forests located at similar latitudes in the Andes of the Chilean Lake District and much lower than old-growth coniferous forests of the Pacific Northwest in North America. Tree species richness was also lower than in other old-growth coastal evergreen forests found in the Coastal Range near Valdivia, at 40°S (Table 8).

**Table 7**

Biplot scores for tree species and constraining variables after obtaining a significant overall trace (after 10,000 Monte Carlo permutations,  $P < 0.005$ ) for the constrained correspondence analysis (CCA) of all forest plots and old-growth plots. CCA1 and CCA2 are constrained axes that accounted for most of the explained variation (species data and species–environment relationship). The best predictors of tree species densities and basal areas along the constrained axes are in bold. Tree species order follows Table 6. Rare species (species occurring only in one site) were excluded from the analysis (see Section 2 for details).

	All plots				Old-growth plots			
	Basal area		Density		Basal area		Density	
	CCA1	CCA2	CCA1	CCA2	CCA1	CCA2	CCA1	CCA2
Explained variation (%)	20.7	12.4	23.9	10.1	23.4	13.6	33.6	9.4
Tree species								
<i>A. punctatum</i>	1.08	−1.00	1.24	−1.63	−0.74	1.00	−0.98	1.33
<i>A. meli</i>	0.08	−0.88	−0.33	−0.53	−0.52	1.10	−1.03	1.53
<i>L. apiculata</i>	1.04	−0.23	1.15	−1.23	−0.67	0.26	−0.85	0.34
<i>M. ovata</i>	0.64	0.24	0.88	−0.15	−0.60	−0.18	−0.91	−0.33
<i>M. planipes</i>	0.40	0.98	0.87	−0.03	−0.63	−1.03	−0.84	−0.64
<i>R. spinosum</i>	0.55	0.20	0.97	−0.58	−0.76	−0.17	−1.01	0.40
<i>W. trichosperma</i>	−1.31	−0.43	−1.00	0.26	1.60	0.35	1.06	0.00
<i>S. conspicua</i>	−1.29	−0.31	−1.01	0.38	1.47	−0.25	0.98	−0.27
<i>N. nitida</i>	−1.12	−0.06	−0.91	−0.08	1.52	0.00	1.04	−0.07
<i>C. hookerianum</i>	−1.19	−0.54	−0.93	−0.32	1.63	0.53	1.15	0.33
<i>P. nubigena</i>	−0.97	−0.22	−0.78	−0.17	1.33	0.27	1.05	−0.02
<i>T. stipularis</i>	−1.27	−0.54	−0.99	−0.18	1.60	0.52	1.13	0.27
<i>M. parviflora</i>	0.23	−0.95	0.15	−0.80	−0.18	0.89	−0.22	0.92
<i>D. winteri</i>	−0.80	0.20	−0.82	−0.05	1.07	−0.25	0.91	−0.02
<i>A. luma</i>	0.39	0.59	0.50	0.70	−0.38	−0.23	−0.27	−0.30
<i>L. philippiana</i>	0.44	0.60	0.82	−0.37	−0.48	−0.63	−0.76	0.22
<i>G. avellana</i>	−0.91	−0.66	−0.41	−0.18	1.16	0.52	0.26	0.27
<i>C. paniculata</i>	−0.12	0.47	−0.90	−0.10	0.05	−0.92	0.99	0.08
<i>E. cordifolia</i>	0.04	−0.82	−0.48	−0.39	−0.14	0.81	−0.44	0.93
Constraining variables								
Distance to coastline	<b>−0.82</b>	0.21	<b>−0.73</b>	<b>0.57</b>	<b>0.72</b>	−0.38	<b>0.75</b>	−0.34
Elevation	0.05	<b>0.75</b>	0.40	0.30	0.15	<b>−0.51</b>	−0.06	−0.47
Mean temperature	<b>0.92</b>	0.09	<b>0.97</b>	−0.05	<b>−0.87</b>	0.15	<b>−0.92</b>	0.10
Mean maximum temperature	<b>0.70</b>	−0.47	<b>0.72</b>	−0.43	<b>−0.60</b>	<b>0.64</b>	<b>−0.70</b>	<b>0.59</b>

Our results also support the view that old-growth forests are often highly variable in structure and tree species composition (Foster et al., 1996). Dbh distributions generally fitted a broad range of functions, as suggested by c-Weibull parameters. Such structural differences among stands may reflect differences in disturbance regimes (Coomes et al., 2003), which in forests presented here vary from light to moderate canopy disturbances (Veblen et al., 1981; Veblen, 1985; Armesto and Fuentes, 1988; Gutiérrez et al., 2004; Gutiérrez et al., 2008). Disturbance regimes (i.e. tree-fall gaps of different sizes generated by emergent and canopy trees) play a fundamental role in producing variable canopy structure of old-growth stands, as documented by the plot MELL1 (50% of its area in canopy gaps). Canopy disturbance may drastically change other structural attributes (e.g. stem density, basal area, and vertical stratification). Because of the differences in life spans among main canopy tree species in North Patagonian and Valdivian forests (Table 3), the stand age criterion should be used with caution. For example, some forest plots which were dominated by *L. philippiana* (MELISA, ELI) coincided in most old-growth criteria, as described above, but their stand age was <150 years and accordingly did not classify as old growth (Table 4). A more precise determination of the time elapsed since the last coarse-scale disturbance would be necessary to assess the old-growth condition in these stands. Dendroecological analysis (Fritts and Swetnam, 1989) provide a valuable tool to conduct such analyses.

Old-growth forests are critical for implementing biodiversity conservation strategies at a regional scale (Hunter and White, 1997). In general, tree species richness was higher in old-growth than in younger stands suggesting an increasing trend in tree species richness with stand age reported for Chiloé Island by Aravena et al. (2002). Additionally, some tree species (i.e. *D. diacanthoides* and *M. chrysocarpa*) were recorded only in old-

growth stands. *D. diacanthoides* is a common species of Chilean temperate rainforest in the mainland (Veblen et al., 1981) but rare in Chiloé Island. It has been suggested that the persistence of this tree species in lowland forests may be threatened by intense anthropogenic disturbance (e.g. fire) (Abarzúa et al., 2006), but we currently have no clue about its possible decline. *M. chrysocarpa* is a common tree species of the understory of old-growth *Fitzroya cupressoides* (Cupressaceae) forests on the coastal range of Chiloé Island.

The high vertical heterogeneity of stands classified as old-growth has been shown to have a positive influence on bird species richness and abundance (Díaz et al., 2005). Old-growth stands often had numerous senescent trees as well as large snags (dbh >20 cm) that are considered key structural elements for forest biodiversity, as they provide habitat for woodpeckers and other cavity nesters (Willson et al., 1996; Cornelius, 2008). Such habitat structures are also important in Subantarctic rain forests (Vergara and Schlatter, 2004) and North American temperate forests (Spies and Franklin, 1991). Furthermore, snags also provide important habitat for a significant diversity of vascular and non-vascular epiphytes (Muñoz et al., 2003; Díaz et al., 2005) and logs offer safe-sites for regeneration of most tree species in these rain forests (Lusk, 1995; Christie and Armesto, 2003).

The ongoing process of forest fragmentation in Chiloé Island, which often is accompanied by substantial changes in forest structure and tree species composition (Echeverría et al., 2007; Jaña-Prado et al., 2007) can compromise the habitat structure provided by old-growth forests. Under this changing scenario, the identification of remnant old-growth stands, especially in accessible areas, is an urgent task for conservation planning. In our study, six of the 17 mature stands sampled did not fit the old-growth structure criteria. This result documents that current national inventories of Chilean forests (CONAF-CONAMA-BIRF,

**Table 8**  
Comparison of structural attributes of old-growth forests in Chile, New Zealand and North America. Sampling method refers to the minimum size of the stems considered.

Forest type	Sampling method	Tree species richness	Stand ages (years)	Density (N/ha)	Basal area (m <sup>2</sup> /ha)	Reference
North American temperate rainforests						
Coniferous Pacific Northwest	d.b.h. >5 cm	5–17	>400	–	98–338	(1)
Douglas-fir forests	d.b.h. >5 cm	4–6	>195	394–551	64–74	(2)
North American temperate forests						
Hemlock – hardwood	d.b.h. >10 cm	2–3	290–390	200–500	50–60	(3)
Quercus – hardwood	d.b.h. >8 cm	5–12	>250	385–590	17–61	(4)
New Zealand temperate rainforests						
<i>Nothofagus</i> – <i>Weinmania</i>	>2 m tall	12	>800	444.7	55.9	(5)
Podocarp/broadleaved	d.b.h. >1 cm	14	>400	6015	144.5	(6)
Chilean temperate rainforests						
<i>Andean forests</i>						
Evergreen broadleaved	d.b.h. >5 cm	8–9	>380	1451–2343	207–305	(7)
<i>Nothofagus</i> – dominated	d.b.h. >5 cm	4	>570	1162–1478	175–273	(7)
<i>Nothofagus</i> – dominated	d.b.h. >5 cm	5	–	501	126	(8)
<i>Nothofagus</i> – dominated	d.b.h. >5 cm	6	>300	200–1200	31–245.8	(9, 10)
Evergreen broadleaved	d.b.h. >5 cm	5	>300	160–1760	43.4–221.3	(9, 10)
<i>Chiloé forests</i>						
Evergreen broadleaved	d.b.h. >30 cm	8–10	>500	271–494	–	(9)
Evergreen broadleaved	d.b.h. >5 cm	8–10	–	883–1179	56–90	(11)
Evergreen broadleaved	d.b.h. >5 cm	5–6	–	1095–1541	77.9–111.3	(12)
Evergreen broadleaved	d.b.h. >10 cm	6–9	200	750–1436	32.3–78.4	(13)
<i>Coastal forests</i>						
Podocarp dominated stand	>2 m tall	7	>200	–	77.7	(14)
Evergreen broadleaved	d.b.h. >5 cm	10–16	–	499–939	63.1–113.8	(15)
North Patagonian forests	d.b.h. >5 cm	7	–	500–690	64.3–94	(16)

Data sources: (1) Waring and Franklin (1979); (2) Spies and Franklin (1991); (3) Ziegler (2000); (4) Orwig et al. (2001); (5) Lusk and Smith (1998); (6) Smale et al. (1997); (7) Pollmann and Veblen (2004); (8) Donoso and Lusk (2007); (9) Veblen (1985); (10) Schlegel and Donoso (2008); (11) Donoso et al. (1984); (12) Donoso et al. (1985); (13) Armesto and Figueroa (1987); (14) Lusk (1995); (15) Donoso and Nyland (2005) and Donoso (2002); (16) Innes (1992) and Donoso (1993).

1999) fail to properly identify old-growth stands. Using their mature forest category will greatly overestimate old-growth forest cover. The attributes of old-growth forests identified here may help to accurately map rapidly declining old-growth forests in southern Chile and adjacent Argentina. These structural attributes of old-growth may also be used to develop forest management protocols aimed at restoring or reproducing old-growth structure in logged or disturbed stands. With regard to hydrologic cycles, the large intercepting surface and evapotranspiration rates of the old-growth forest canopy (Díaz et al., 2007) in this high rainfall area may be relevant to regulating soil water infiltration and maintaining the depth of the water table in poorly drained sites of Chiloé Island and the Lake District.

#### 4.2. Environmental gradients

According to bi-plots of tree species (Fig. 4, Table 7) a high degree of variance was explained by a well-defined floristic dichotomy between Valdivian and North Patagonian rain forest species, which is mainly driven by differences in the mean air temperature among sites occupied by each forest type. This dichotomy is consistent with previous studies of forest composition in this region (Veblen et al., 1983; Villagrán, 1991; Armesto et al., 1996). Floristic differences were associated primarily with latitudinal and altitudinal gradients in the Chilean Lake District (Schmithüsen, 1956; Oberdorfer, 1960; Villagrán, 1991, 2001). Valdivian rain forest species are classified as thermophilic (i.e. *E. cordifolia*, *A. punctatum*), some are thermally intermediate (*N. nitida*, *W. trichosperma*, *L. philippiana* and Myrtaceae species) and North Patagonian species are classified as cold-resistant (Podocarpaceae species, *D. winteri*, *T. stipularis*) (Heusser et al., 1999). Our results were also consistent with morphological adaptations of North Patagonian tree species to cold temperatures (e.g. high plasmatic resistance to desiccation and a high sclerophyll index of

leaves) and/or acclimation to winter temperatures (Alberdi, 1995). Further sampling should be conducted especially in the North Patagonian forest type to characterize variation of its floristic composition and stand structure along climatic and edaphic gradients.

Structural variability among old-growth forest stands of Chiloé Island was also related to site differences (e.g. air temperature, coastal vs. non-coastal, edaphic conditions). In coastal sites the dominance of *A. punctatum* may be related to its ability to tolerate salt spray (Pérez, 1994). In contrast, *W. trichosperma* and *P. nubigena* are rare in coastal areas (Donoso et al., 1985; Veblen, 1985; Gutiérrez et al., 2008). Basal area of *E. cordifolia* seemed unresponsive to the temperature gradient, but more responsive to elevation differences. It has been suggested that enhanced soil drainage on hillsides improves the performance of *E. cordifolia* (Donoso et al., 1984; Donoso, 1993). The association of *P. nubigena*, *D. winteri*, *N. nitida* and *T. stipularis* is more characteristic of poorly drained soils (Armesto et al., 1995; Lusk, 1996a) and in soils characterized by high C/N ratios and lower N availability (Pérez et al., 1998; Pérez et al., 2004).

#### 4.3. Long-term research in old-growth forests

Old-growth forests are priority sites for ecological monitoring because they can be used to test hypotheses about complexity, stability, resilience, and ecosystem change (Hendrickson, 2003). Few studies in southern Chile have compared old-growth stands to young stands with regard to structural attributes, composition and ecosystem functions (Aravena et al., 2002; Carmona et al., 2002; Pérez et al., 2004). Changes in stand structure and species composition over time (Laurance et al., 2006), demographic rates of tree species (Lorimer et al., 2001; van Mantgem et al., 2009), and canopy turnover (Runkle, 2000) remain poorly documented for temperate rainforest of southern Chile. Most monitoring experi-

ments (Lara et al., 2000) have been conducted to test silvicultural practices in second-growth stands, particularly to follow tree growth and regeneration. The present study contributes to identifying state variables of significant ecological value for old-growth forests in Chiloé Island, based on a pilot permanent plot network. This network provides a useful baseline for addressing the dynamic behaviour of unmanaged forests in the face of prospective climate change, biotic effects of herbivores and pathogens, and rapid changes in land use. Additionally, old-growth forests characteristics described here can serve as natural models to restore critical structural features to second-growth, managed, or highly degraded forests (Foster et al., 1996) or for developing management strategies focused on native tree species and uneven-aged forest structures (Rüger et al., 2007).

## 5. Conclusions

Characterization of old-growth forests is necessary because of their current decline due to changes in land use. Valdivian and North Patagonian old-growth forests in Chile showed a distinctive structural heterogeneity and floristic diversity influenced both by stand age and disturbance history of the stands. Structural heterogeneity was also related to environmental differences among sites (e.g. air temperature, coastal vs. non-coastal, soil types). To prevent the rapidly declining trend in old-growth forest area in Chile, which affects their role as repositories of species genetic information, carbon stores, biodiversity, and sources of baseline data on the dynamics and biogeochemical function of forest ecosystems, it is necessary to recognize their status and educate the public on understanding their unique ecological values. Such recognition should be manifested in future national inventory which should assess the changes in cover of threatened remnants of old-growth forest stands at regional and local scales.

## Acknowledgements

We acknowledge the landowners that allowed us to work in their forests, the Armada de Chile for access to climatic data, and CONAF (Santiago) for GIS data from Chiloé Island. We thank M. Fuentes, C. Mellado, V. Levín, R. Valenzuela, M. Cona, M.F. Salinas, M. Nuñez-Avila and M.A. Martínez for field and laboratory assistance. The students of Forest Ecology field classes of 2002–2005 helped with permanent plot sampling. Two anonymous reviewers provided useful comments. Financial support was provided by Contract ICA 4-CT-2001-10095 Biocores project funded by EC under INCO IV programme, Millennium Scientific Initiative project P05-002 to IEB, Fondecyt grants 1050830 (2005), and FONDAP 1501-0001 to the Center for Advanced Studies in Ecology and Biodiversity, and a DAAD fellowship to AGG. This is a contribution to the research program of Senda Darwin Biological Station, Ancud, Chiloé.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2009.03.011.

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