ORIGINAL ARTICLE

Effects of natural and human disturbances on the dynamics and spatial structure of *Nothofagus glauca* in south-central Chile

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ABSTRACT

Aim The general model for *Nothofagus* regeneration dynamics states that the species of this genus tend to occur in frequent, coarse-scale disturbance sites and/or in harsh conditions. The aim of this study is to test this regeneration model in deciduous mediterranean *Nothofagus glauca* forests at the northern limit of range of this genus, which include some of the most diverse but least well understood forests in the region. The study also aimed to advance general understanding of the ecological role of *N. glauca* in these forests, and its response to disturbance, by examining the composition, structure and regeneration patterns of *N. glauca* forests in the mediterranean zone following three different disturbance histories: mature, post-logging, and post-landslide second growth.

Location The study was conducted at the southern limit of the mediterranean climatic zone, in the foothills of the Andes (36°35′ S, 71°28′ W) in south-central Chile, near the south limit of range of *N. glauca*. Study sites were located at a range of altitudes between 660 and 850 m a.s.l.

Methods Two fully mapped 0.12–0.14-ha plots were located at each of three sites in order to sample age, composition, structure, canopy density and spatial patterns of the stands. The spatial description of sites was estimated with point-pattern analysis using Ripley's *L*-function (univariate and bivariate versions). Shannon's index was used to account for stand structural diversity by height class. Leaf area index (LAI) and canopy density were assessed with fisheye digital photos.

Results *Nothofagus glauca* was the dominant canopy tree species at all sites. In the mature site there was abundant regeneration of *N. glauca* saplings, leading to a complex open canopy and an all-aged structure with a total basal area (BA) of 21–33 m^2 ha^{-1} (including all tree species), despite the presence of shade-tolerant tree species and the bamboo *Chusquea cumingii*. The canopy was complex (Shannon's index up to 1.7), but was relatively open (16%). There was no evidence of a shift in regeneration from shade-intolerant *Nothofagus* species towards more shade-tolerant species. In the post-logging secondary growth stand an evenly aged structure prevailed, with patchy, more open canopies (15–21%, total BA = 9–38 m^2 ha^{-1}), but with a less diverse canopy structure. The last site, located in the debris fan of a landslide, presented the lowest LAI and highest canopy opening (23–30%) where the site occupancy is not yet complete (total BA = 14–23 m^2 ha^{-1}). At the harshest sites, saplings had a positive spatial association with adult trees, which suggests facilitation from adult trees to saplings.

Main conclusions Our study supports the general model for *Nothofagus* regeneration dynamics, except that *N. glauca* does not attain sufficient canopy density to require disturbance for regeneration, even in the best sites. *Nothofagus*

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glauca can be both a pioneer in harsh site conditions, as well as a gap strategist in mature forests. In these generally harsh sites, the most species, the densest canopies and the most diverse structures occur in the oldest forests. Low canopy density allowed for diverse understorey species at all sites.

INTRODUCTION

A general model has been proposed for describing variation in the regeneration dynamics of *Nothofagus* species in southern Chile, including disturbance regime, site conditions and the shade-intolerance characteristics of each species (Veblen *et al.*, 1996; Pollmann & Veblen, 2004). *Nothofagus* species are located either at sites with environmental conditions restrictive for other tree species (high latitudes, high elevations or edaphically suboptimal sites), or at more favourable sites with periodic disturbances that vary in magnitude (Veblen & Ashton, 1978; Read & Hill, 1985). Patterns of stand development in Chilean *Nothofagus* forests are relatively well known for the southern area of the country, and are the result of both coarse-scale catastrophic disturbances (primarily mudslides, windstorms and tectonic activity) producing whole-stand replacement, and small tree falls resulting in fine-scale gap dynamics (Donoso, 1993; Veblen *et al.*, 1996; Pollmann & Veblen, 2004). In order to improve the representational range of this genus, more evaluation and testing of this general model are needed for the different *Nothofagus* forest types. There is little information, for instance, on the diversity of *Nothofagus* forests located at their northernmost distribution in Chile, the mediterranean zone (Donoso, 1996). We need to know if these forests are a result of catastrophic or chronic disturbances, and the nature of competitive relationships between dominant species. For instance, it is unclear if mediterranean *Nothofagus* species require large disturbances for regeneration, and whether or not it can retain dominance after tree-fall gaps are created.

Among the *Nothofagus* species occurring in the mediterranean zone of Central Chile, *Nothofagus glauca* (Phil.) Krasser is considered one of the dominant tree species (Donoso, 1996). Nonetheless, *N. glauca* has been classified as a vulnerable species (Benoit, 1989) due to the many human-influenced transformations of its habitat conditions, particularly through logging and conversion to *Pinus radiata* plantations (Donoso, 1993). Once again, there is little information on the structure and dynamics of these forests, and therefore it has been difficult so far to develop effective conservation and sustainable management strategies for this species (Donoso, 1996; Litton & Santelices, 1996; Amigo *et al.*, 2000).

Recent work in northern temperate forests emphasizes the key role that spatial structure can play in providing insights to the complex processes of stand establishment and species interactions following disturbances (Ford & Sorrensen, 1992; Tilman & Kareiva, 1997). During the development of a stand, for example, the distribution of trees should reflect the ability of individuals to survive competition and dominate the initial patches (Lorimer *et al.*, 1988; Oliver & Larson, 1996). While it may be difficult to infer ecological processes from these observed spatial patterns (Cale *et al.*, 1989), these data can provide a basis for generating hypotheses about underlying processes (Liebhold & Gurevitch, 2002) such as species co-existence; the quantification of overstorey–understorey relationships; and the importance of competitive/facilitative interactions. We know, for example, that mature *N. glauca* forests are richly diverse and include a complex understorey structure (Amigo *et al.*, 2000). However, it is unclear how these spatial structures are established or maintained in *N. glauca* forests.

Furthermore, one of the greatest challenges facing ecologists and silviculturists lies in elucidating and modelling the factors determining vegetation pattern and ecosystem processes of native forests at the landscape scale. One of the first basic pieces of information needed for management and/or conservation of any forest is to determine patterns of forest dynamics and its relationship to disturbance agents. Available descriptors of disturbance regimes are only partial, and usually deal with a single type of disturbance such as tree fall or fire (Veblen, 1992). To understand the role of disturbance in the forest dynamics of a specific tree species, the full range of disturbances affecting it should be considered. Quantitative forest structure data relative to disturbance factors affecting *Nothofagus* species dynamics are scant in the mediterranean zone of south-central Chile.

In this study, we characterize and compare tree composition, structure, and spatial patterns of *N. glauca* second-growth stands with three contrasting disturbance histories, with the aim of obtaining an understanding of how this species develops under the impact of different disturbance agents, and how its spatial structure (particularly with other species) can help to define hypotheses on species co-existence and stand dynamics. The first stand corresponds to a mature stand (120–140 years old); the second has developed after logging and fire application (*c.* 20 and 40 years ago); and the third developed after catastrophic disturbance (a landslide in 1936). With this variety of disturbance histories, we were interested in

answering the following questions: (1) Do *N. glauca* regeneration dynamics and stand development fit the general model developed for southern *Nothofagus* species? (2) Do these forests have episodic or chronic regeneration patterns? (3) Does the presence of *N. glauca* influence the occurrence of tree and understorey species? (4) What is the effect of different disturbance agents on the current composition and structure of these stands? and (5) What is the successional status of *N. glauca*?

METHODS

Study area

The study was carried out at Bullileo sector (36°35′ S, 71°28′ W), San Fabián de Alico, in the southern limit of the mediterranean climate zone, just north of Ñuble River, Ñuble Province (Region VIII) in the Andean foothills of south-central Chile (Fig. 1). This sector also constitutes the southern limit of *N. glauca* (Amigo *et al.*, 2000). This area belongs to the Mesomediterranean belt with perhumid climatic conditions characterized by mild winters and dry summers (Donoso, 1996; Amigo & Ramírez, 1998), with almost 80% of the annual precipitation of 1051 mm occurring between May and September. Monthly mean minimum temperatures range from 3.8 °C in July to 11 °C in January, and monthly mean maximum temperatures range from 12.3 °C in July to 28.4 °C in January (Estación Meteorológica Universidad de Concepción, Chillán; 180 m a.s.l., 70 km from the study sites). The soils are shallow with a predominance of volcanic material including andesitic and basaltic materials (Donoso, 1996).

Field methods

Two 0.12–0.14-ha plots were located randomly within each of the three disturbance type sites (hereafter denoted as mature, logged and landslide sites) where *N. glauca* was the dominant species. The exact locations of plots were chosen at random within stands that were reasonably accessible. Species nomenclature follows Marticorena & Quezada (1985). We inferred stand development and disturbance history from population age and size structures of the different plots. We also used the spatial location of trees to infer interactions among species and size classes.

In each plot, all trees > 50 cm tall were mapped and measured. The co-ordinates of the estimated centre of each
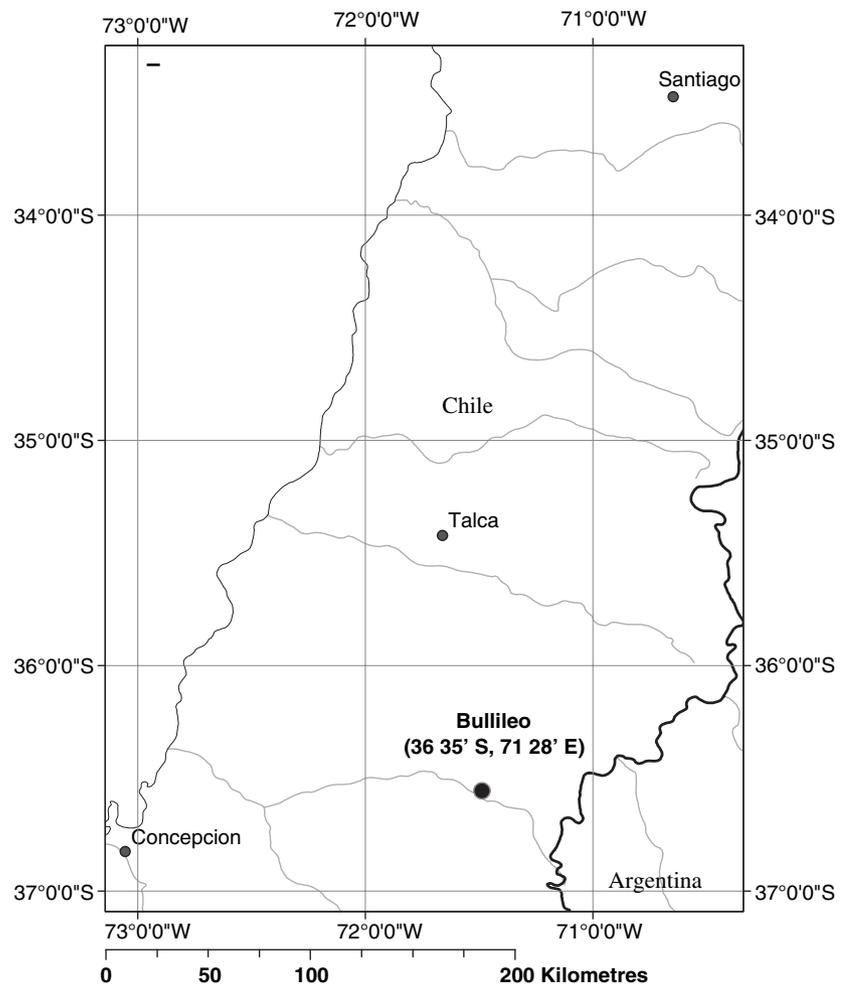

Figure 1 Partial map of Chile, including the sampling location at Bullileo sector, San Fabián de Alico, Ñuble province, central Chile. The three sites sampled are no more than 5 km apart.

tree and sapling (< 5 cm d.b.h. and taller than 1 m) stem were recorded using a handheld laser range finder (Forest Pro, Laser Technology, Centennial, CO, USA) and a digital compass, which estimate the distance and azimuth to the centre of each tree (> 0.5 m tall) to the nearest 1 mm. Field measurements were converted to co-ordinates using trigonometric functions. For each mapped tree stem, the species, height and d.b.h. (diameter at 1.35 m above ground) were measured. Heights were measured using a clinometer. To determine ages, we worked with all the tree cores of one plot per site (mature site plot 1; landslide site plot 2), and more than 50% of the trees in the logged site plot 1. Tree cores were dried, mounted in grooved wooden boards and sanded with successively finer grades of sandpaper to reveal annual rings. Annual rings were hard to read, so phloroglucinol was used to stain rings, and rings were counted using a dissecting microscope (Patterson, 1961). For cores that missed the pith of the tree, procedures described by Duncan (1989) were used to estimate the number of missing rings. No correction was applied for time required to grow to coring height (20 cm).

We assessed canopy density and projected leaf area index (LAI) for the different plots with fisheye lens canopy digital photographs. Twelve photographs were taken per plot in February 2004 with a 7-mm Nikon f7.4 fisheye lens, mounted on a Nikon Coolpix 950 digital camera. The lens has an orthographic projection of 180° angle of view. The camera was mounted 30 cm above ground on a tripod, levelled and oriented to true north, looking upwards through the canopy. We used the GLA (GAP LIGHT ANALYZER ver. 2) software (Frazer *et al.*, 2000) to process the photographs and to compute percentage canopy openings and LAI.

Data analysis

Stand structure was determined from stem diameter and age distributions at each plot. Stem density and basal area (BA) were scaled up to 1 ha. For each tree species, a relative importance value was computed as an average of the relative density and relative dominance (BA) (Orwig *et al.*, 2001; Pollmann, 2002). Diameters of trees were grouped into 10-cm size classes for *N. glauca* and for all species combined in each plot. Similarity between size- or age-class mean values, and distributions of these variables among plots, were measured with the Mann–Whitney *U*-test and Kolmogorov–Smirnov test by ranks, respectively (Sokal & Rohlf, 1995). Spearman's rank correlation analyses (diameter and age data were not normally distributed: Kolmogorov–Smirnov one-sample test) were performed to determine if there were significant correlations between tree diameter and age for *N. glauca*. To test for significant differences among plots for canopy opening and LAI, the data obtained were analysed by one-way ANOVA; multiple comparisons were conducted by Scheffé test (Sokal & Rohlf, 1995). Canopy-opening values were log-transformed and LAI values were square-root-transformed to achieve homogeneity of variances. All these analyses were carried out with SPSS (2000).

Shannon's diversity index was used to estimate species and structural diversity by grouping species abundance (BA) by height class. Shannon's index, H', is originally defined as follows:

$$H' = -\sum_{i=1}^{S} p_i \times L_n \times p_i$$

where p_i is the proportion of individuals in the *i*th species, and *S* is the number of species (McCune & Grace, 2002). This index basically measures the 'information content' for a sample unit in terms of uncertainty; the more uncertainty one has about the species of an individual, the higher the diversity of the community. First, we used Shannon's index to estimate species diversity per plot, by accounting for the proportion *N. glauca* represented in number of individuals (p_i) per 2-m height class. Second, we used Shannon's diversity index to estimate structural diversity by using the proportion of BA per ha (p_i – relative basal area, RBA) per species (*S*) (Staudhammer & LeMav, 2001).

Spatial pattern analysis

In analysing regeneration processes it is often useful to account for spatial patterns of trees, particularly by mapping individual trees at different scales (Veblen, 1992). Co-ordinate data (*x*, *y*) were collected for every tree to determine the univariate spatial pattern (distribution) for each species, and the bivariate spatial pattern (association) between species and tree classes at each plot using a modified version of Ripley's *K*-function (Lotwick & Silverman, 1982).

To analyse spatial point patterns, under the assumption of stationarity (the process must be invariant under translation) and isotropy (invariance under rotation), we chose the *L*-function, $L(t) = \sqrt{(K(t)/\pi)} - t$, proposed by Bessag (1977), which is a linearized version of Ripley's *K*-function (Ripley, 1977), and is preferred for interpretation's sake. The original Ripley's *K*-function is based on the variance (second-order analysis) of all point-to-point distances in a two-dimensional space, and gives a description of spatial structure at different scales at the same time (Cressie, 1993). The *L*-function is estimated as: $\hat{L}(t) = \sqrt{(K(t)/\pi)} - t$. The *L*-function transformation makes $K(t)$ linear in *t* (distance), and scales its variance to facilitate testing against the null hypothesis of complete spatial randomness (it is assumed that all points are distributed independently). The linearized function has an expectation of zero for any value of *t* when the pattern is random. The spatial pattern can then be described as clumped, random or regular at any distance *t* up to half the length of the shortest rectangular plot side if the calculated $\hat{L}(t)$ is greater than, equal to or lower than the 99% confidence envelopes, respectively (Dixon, 2002). For this analysis, *N. glauca* individuals were divided into three categories: saplings, juveniles (d.b.h. 5–15 cm) and adults (d.b.h. > 15 cm). The statistical significance of the departure from zero was tested using a Monte Carlo procedure that randomly repositions all points in the plot and generates $L(t)$ functions. In this study we

computed a 99% confidence interval by running 99 simulations at intervals of 1 m from 1 to 16 m (half the length of the shortest side of the plot). The Cramer–von Mises test was used to account for significance (Haase, 2002). Since edge effects become a concern at greater distances, we used weighting edge-correction methods to account for this effect (Haase, 1995).

To estimate the spatial association between species and tree classes at each plot, we used the bivariate spatial function $K_{1.2}(t)$ (a derivation from the univariate spatial function), which characterizes the relative location of one type or class (species or size class 1) with respect to another (class 2). Following the logic used above, we used the modified $L_{1.2}(t)$-function (Lotwick & Silverman, 1982), whose classical estimator is $\hat{L}_{1.2}(t) = \sqrt{(\hat{K}1.2(t)/\pi)} - t$. $\hat{L}_{1.2}(t)$ provides evidence of spatial association between species 1 and 2: if the value of $\hat{L}_{1.2}(t)$ is not significantly different from zero, the null hypothesis that the two species have independent spatial distribution cannot be rejected (Goreaud & Pélissier, 2003). Monte Carlo simulations were used to evaluate the statistical evidence of a departure from zero; we built 99% confidence intervals from 99 shifts of one class of trees with respect to the other. Values of $L_{1.2}(t)$ greater than, equal to or lower than 99% confidence envelopes indicated significant positive spatial association (attraction), spatial independence and significant negative spatial association (repulsion), respectively, between the two tree classes analysed (Dixon, 2002; Goreaud & Pélissier, 2003). The spatial statistics program SPPA.EXE (Haase, 2002) was used for computation of both univariate and bivariate analyses.

RESULTS

Stand structure

All of our *N. glauca*-dominated study sites have a diverse size structure, particularly for the mature and landslide sites. Diameter distributions for these two sites included abundant saplings, generally with declining numbers of individuals in successively larger diameter classes, exhibiting a negative exponential or reverse-*J* pattern, typical of unevenly aged forests (Kolmogorov–Smirnov one-sample test; Fig. 2a,c). For instance, in the mature site, stems < 5 cm d.b.h. accounted for *c.* 46% and 76% of plot 1 and 2 populations, respectively. In contrast, the two plots from the logged site exhibited a normally shaped diameter distribution, accounting for *c.* 42% and 79% of their stems in middle size classes (9.5–15 cm d.b.h.) for logged site plots 1 and 2, respectively (Kolmogorov–Smirnov one-sample test; Fig. 2b). Age–diameter relationships were highly significant for all three sites ($R^2 = 0.93$, 0.73 and 0.67 for mature, logged and landslide sites, respectively; Fig. 3). Hence we considered size data sufficient to explain stand structure for all the sites. Donoso *et al.* (1984) and Veblen (1985) also found highly correlated age–diameter relationships for temperate rain forests. Across the different sites, *N. glauca* represented an all-aged population, forming the oldest tree cohorts: recruited *c.* 1860 (mature site plot 1); 1880 (mature
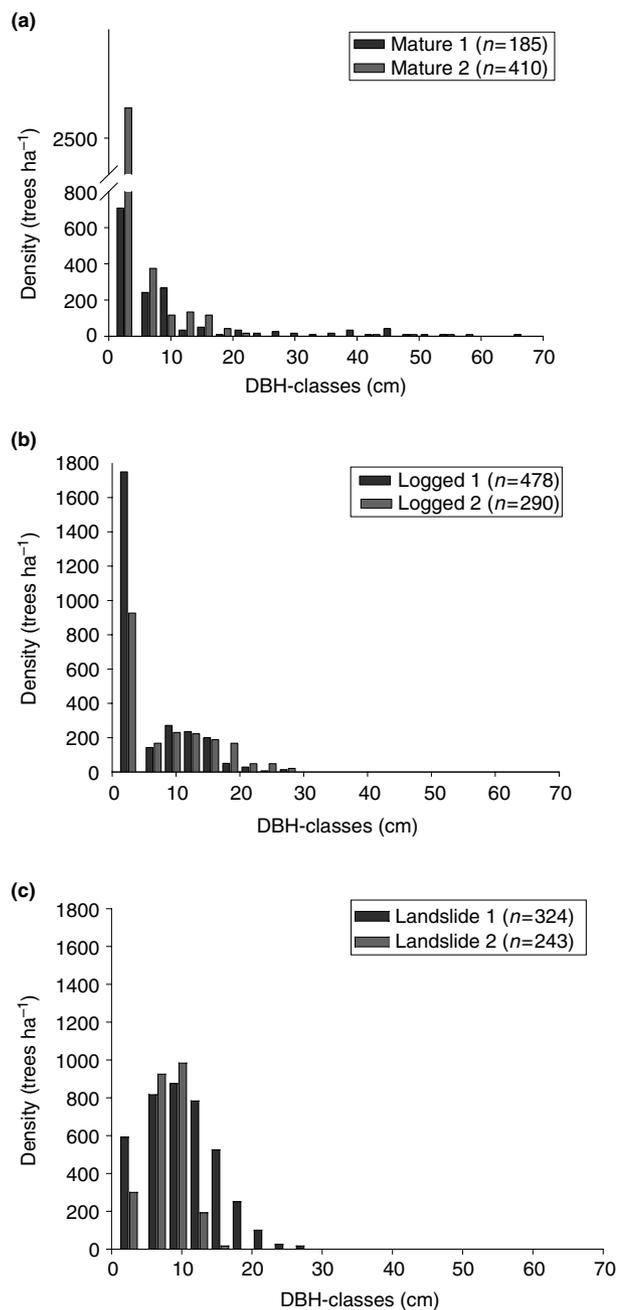
Figure 2 Diameter size-class frequency distribution for the three sites in Bullileo sector, San Fabián de Alico, Chile: (a) mature stand; (b) logged stand; (c) landslide stand.

site plot 2); 1960 (logged site plot 1); 1987 (logged site plot 2); and 1940 (landslide site). Basal area across most of the study sites was moderate (21.4–37.8 m² ha⁻¹), and low for logged site plot 2 and landslide site plot 2 (9.34 and 14.3 m² ha⁻¹, respectively).

Stand composition

At all three study sites, *N. glauca* was the dominant tree species (highest relative importance value; Table 2). At sapling level,

(a)

Mature 1 (*n* = 103)

Age = 2.2296*dbh + 7.8891; R^2 = 0.9328

(b)

Logged 1 (*n* = 70)

Age = 1.2209*dbh + 5.7907; R^2 = 0.7271

(c)

Landslide 2 (*n* = 145)

Age = 1.9788*dbh + 10.008; R^2 = 0.6736

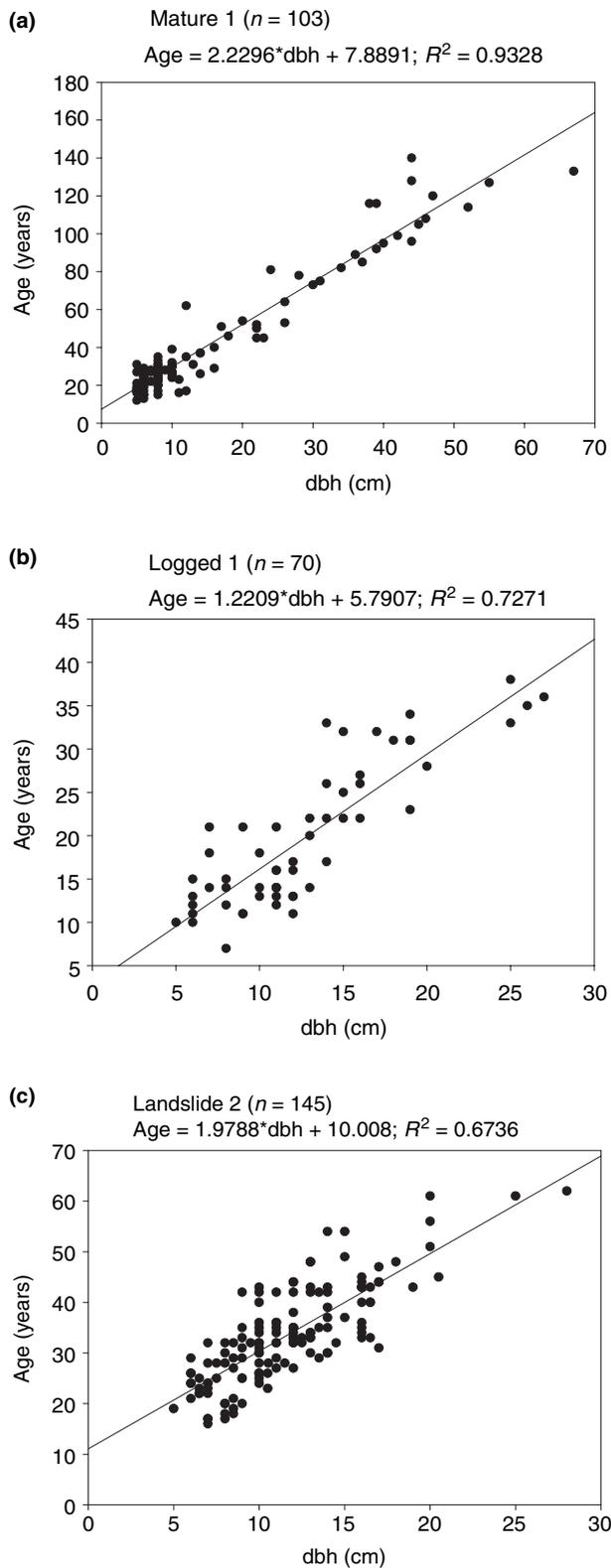**Figure 3** Relationships between diameter at breast height (d.b.h., 1.35 m) and age for one plot per site for *Nothofagus glauca* in Bullileo sector, San Fabián de Alico, Chile: (a) mature stand; (b) logged stand; (c) landslide stand.
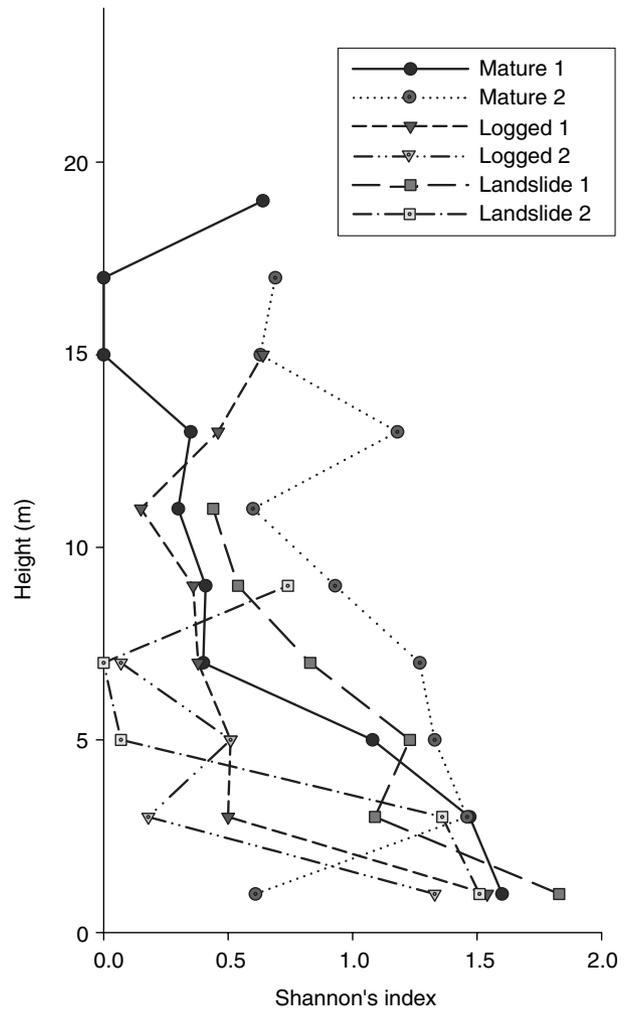
Figure 4 Relationship between Shannon's diversity index for species diversity by height class using species abundance data across all *Nothofagus glauca* stands at Bullileo sector, San Fabián de Alico, Chile.

N. glauca had densities of 300–2042 saplings ha^{-1} (relative densities of 17.9–48.9%; Table 4). Plant species composition was markedly different among the study sites, especially for saplings (Fig. 4). Within the tree stratum, mature site plot 2 exhibited the greatest overall diversity, particularly for shade-tolerant species [highest Shannon's diversity index (1.7), Tables 1 and 2]. *Gevuina avellana* was well represented at the mature site plots 1 and 2, logged site plot 1, and landslide site plot 1 (relative importance values 3.8%, 9.2%, 11.6% and 9.7%, respectively). *Cryptocaria alba* had the highest relative importance value (11.9%) after *N. glauca* in mature site plot 2 (Table 2). The landslide site presented the lower diversity for the tree stratum (Shannon's diversity index = 0.043). At the tree sapling–shrub stratum, *Azara serrata*, *Pernettya mucronata* and *Sophora macrocarpa* dominated in mature site plot 1; *G. avellana*, *Sophora mayu* and *Chusquea cumingii* Nees dominated in mature site plot 2. For logged site plot 1, the most frequent saplings were *G. avellana* and *A. serrata*, and for logged

Table 1 Site characteristics of each plot sampled at Bullileo (36°35′ S, 71°27′ W), San Fabián de Alico, Chile

Plot	Altitude (m)	Aspect	Slope (%)	Plot size (m²)	Canopy opening* (%)	LAI* (m² m⁻²)	Shannon index†
Mature 1	850	E	40	1200	16.18 (0.67)	2.06 (0.087)	0.443
Mature 2	710	NE	15	1200	15.63 (0.84)	2.12 (0.094)	1.189
Logged 1	700	S	12	1400	14.65 (0.91)	2.63 (0.088)	0.437
Logged 2	680	S	15	1350	21.09 (1.01)	1.59 (0.078)	0.045
Landslide 1	680	S	10	1200	22.67 (0.50)	1.51 (0.036)	0.489
Landslide 2	660	S	10	1200	29.92 (1.72)	1.11 (0.088)	0.043

*For canopy opening and projected leaf area index (LAI), mean and standard error (in parentheses) are presented.

†Shannon index was applied for stand structural diversity based on basal area per species.

Table 2 Density (trees ha⁻¹), basal area (m² ha⁻¹), relative density and relative basal area for trees > 5 cm d.b.h., for all the plots in Bullileo sector, San Fabián de Alico, Chile

Plot	Density	Relative density	Basal area	Relative basal area	Relative importance value*
Mature 1					
Nothofagus glauca	850	88.7	29.3	88.5	88.6
Nothofagus obliqua	8.3	0.1	1.1	3.3	1.7
Nothofagus leoni	16.7	1.7	2.4	7.3	4.5
Gevuina avellana	66.7	7.0	0.2	0.6	3.8
Azara serrata	8.3	0.1	0.02	0.1	0.1
Persea lingue	8.3	0.1	0.02	0.1	0.1
Total	958		33.1		
Mature 2					
N. glauca	841.7	49.7	13.8	64.6	57.2
N. obliqua	100	5.9	3.5	16.4	11.1
N. leoni	66.7	3.9	0.7	3.3	3.6
G. avellana	241.7	14.3	0.9	4.2	9.2
A. serrata	91.7	5.4	0.3	1.4	3.4
P. lingue	25	1.5	0.2	0.9	1.2
Cryptocaria alba	266.7	15.8	1.7	8.0	11.9
Lomatia dentata	41.7	2.5	0.2	0.9	1.7
Aextoxicum punctatum	16.7	1.0	0.06	0.3	0.6
Total	1692		21.4		
Logged 1					
N. glauca	2957.1	88.8	32.4	85.8	87.3
G. avellana	321.4	9.7	5.1	13.6	11.6
A. serrata	50.0	1.5	0.3	0.7	1.1
Total	3329		37.8		
Logged 2					
N. glauca	1770	99.2	9.3	99.3	99.2
G. avellana	7	0.4	0.01	0.1	0.3
A. serrata	7	0.4	0.05	0.6	0.5
Total	1784		9.34		
Landslide 1					
N. glauca	1308	77	21.0	88.2	82.6
G. avellana	208	12.3	1.7	7.2	9.7
Lithraea caustica	58	3.4	0.2	1.0	2.2
Lithraea hirsuta	100	5.9	0.6	2.7	4.2
L. dentata	18	1.0	0.2	0.8	0.8
C. alba	8	0.4	0.02	0.1	0.2
Total	1700		23.72		
Landslide 2					
N. glauca	1083	95.0	13.6	99.2	97.1
Austrocedrus chilensis	8.3	5.0	0.7	0.7	2.9
Total	1092		14.3		

*Relative importance values were calculated as (relative density + relative basal area)/2.

site plot 2, *S. mayu*, *Baccharis confertifolia* and *Lithraea caustica* were the most common. *Baccharis confertifolia* and *L. caustica* dominated the shrub layer in the landslide site (Table 2).

Canopy structure

Logged site plot 1 had a significantly lower canopy opening (14.65%) and higher projected LAI (2.63 m^2 m^{-2}) when compared with the rest of the sites ($P < 0.005$, Table 1 vs. Table 3). The opposite was found for landslide site plot 2, with a significantly higher canopy opening (29.92%) and lower projected LAI (1.11 m^2 m^{-2}; Table 1) than the rest of the sites ($P < 0.01$; Table 3). At the other two sites (mature and logged) there were no significant differences in canopy structure within

a site, but between these two sites we found a significant difference in canopy opening and projected LAI. The upper canopy layer was dominated by *N. glauca* for most of the sites (*Nothofagus obliqua* for mature site plot 2), achieving maximum heights in mature site plot 1 of *c.* 19 m. These heights are below the maximum heights documented by Donoso (1996), which are close to 30 m. Mature site plot 2 presented the highest structural diversity (highest Shannon's values through height; Fig. 4), while the logged site had the lowest values.

Spatial pattern distributions and associations

The spatial distribution of *N. glauca* tree stems differed by size classes at most sites (Table 5), displaying mostly random spatial distributions for trees > 15 cm d.b.h. Logged site plot 1, however, resulted in a clumped spatial distribution through all *N. glauca* size classes. For smaller d.b.h. classes (5 and 15 cm) and saplings, the spatial distribution was significantly clumped for most distance classes ($P < 0.01$). Companion species showed significant clumpiness across all distance classes for both trees and saplings. Overall, we found strong evidence for a positive association between saplings and adult trees of *N. glauca* belonging to d.b.h. class 5–15 cm. For overstorey trees > 15 cm d.b.h. the association pattern is not clear, having some positive association at a larger scale: 13, 9, 13 and 10 m for mature site plot 2, logged site plot 1, and landslide site plots 1 and 2, respectively (Table 6). There was an independent spatial association mostly between adult trees > 15 and 5–15 cm d.b.h. (but see landslide site plot 2). At mature site plot 2, both adult trees and saplings of *N. glauca* were independently associated with *N. obliqua* and *N. leonii* ($P > 0.05$).

Table 3 Comparisons between (log-transformed) canopy opening (above diagonal) and projected (square-root-transformed) leaf area index (LAI, below diagonal) based on Scheffé multiple comparison test significance values (differences after one-way ANOVA) among plots

Plots	Mature 1	Mature 2	Logged 1	Logged 2	Landslide 1	Landslide 2
Mature 1		−0.018	**0.106**	**0.114**	**0.149**	**0.264**
Mature 2	0.020		**0.123**	**0.132**	**0.167**	**0.282**
Logged 1	**0.159**	**0.179**		0.008	0.044	**0.158**
Logged 2	**0.173**	**0.193**	0.014		0.035	**0.150**
Landslide 1	**0.204**	**0.224**	0.045	0.031		**0.115**
Landslide 2	**0.387**	**0.406**	**0.228**	**0.213**	**0.183**	

Bold type represents significant differences ($P < 0.05$).

Table 4 Saplings (> 1 m tall and < 5 cm d.b.h.) abundance (stems ha^{-1}) within study sites in Bullileo sector, San Fabián de Alico, Chile

Species	Mature 1	Mature 2	Logged 1	Logged 2	Landslide 1	Landslide 2
Nothofagus glauca	2042 (43.0)	1108 (17.9)	614.3 (29.4)	2160.3 (48.9)	591.7 (18)	300 (22.5)
Nothofagus obliqua		50 (0.8)				
Nothofagus leonii		66.7 (1.1)				
Gevuina avellana	333.3 (7.0)	541.7 (8.8)	635.7 (30.4)	223 (5.1)	300 (9.1)	
Azara serrata	491.7 (10.4)	166.7 (2.7)	535.7 (25.6)	369.3 (8.4)	108.3 (3.3)	50 (3.8)
Pernettya mucronata	558.3 (11.8)					
Cryptocaria alba		91.7 (1.5)				8.3 (0.6)
Lomatia dentata	75 (1.6)	25 (0.4)	64.3 (3.1)			
Bacharis spp.	141.7 (3.0)				691.7 (21)	208 (15.6)
Sophora mayu	741.7 (15.6)	391.7 (6.3)	128.6 (6.1)	1351.9 (30.6)	450 (13.7)	258 (19.4)
Chusquea cumingii	341.7 (7.1)	3692 (59.8)		139.4 (3.2)	16.7 (0.5)	
Persea lingue	25 (0.5)					
Luma apiculata		8.3 (0.1)				
Lithraea caustica		16.7 (0.3)	14.3 (0.7)	41.8 (1.0)	866.7 (26.3)	450 (33.7)
Maytenus boaria		16.7 (0.3)				
Lomatia hirsuta			92.9 (4.4)	132.4 (3.0)	258.3 (7.9)	50 (3.8)
Quillaja saponaria						8.3 (0.6)
Aristotelia chilensis			7.1 (0.3)			
Austrocedrus chilensis					8.3 (0.3)	
Total	4750	6175	2092.9	4418	3292	1333

Values in parentheses are relative density.

Table 5 Patterns of spatial distribution based on the univariate *L*-function for tree classes of *Nothofagus glauca* and the group of companion species through all the study sites in Bullileo sector, San Fabián de Alico, Chile

N. glauca, d.b.h. > 15 cm — Distance *t* (m) | *N. glauca*, d.b.h. 5–15 cm — Distance *t* (m)

Plots	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	P†	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	P
Mature 1	33																0.720	65	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Mature 2	23																0.289	78	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Logged 1	87	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c*	**0.001**	325	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Logged 2	1	=	=	=	=	=	=	=	=	=	=	=	=	=	=	=		254	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Landslide 1	53																0.220	104	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Landslide 2	31																0.981	102	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**

Companion species, d.b.h. > 5 cm — Distance *t* (m) | *N. glauca* saplings, d.b.h. < 5 cm — Distance *t* (m)

Plots	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	P	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	P
Mature 1	103	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**	244	c	c	c	c	c	c	c	c	c	c	c	c	c			**0.001**
Mature 2	160	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**	131	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Logged 1	62	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**	83	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Logged 2	0	=	=	=	=	=	=	=	=	=	=	=	=	=	=	=		310	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Landslide 1	45	c	c	c	c	c	c	c	c	c			c	c	c	c	**0.001**	70	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Landslide 2	54	c	c	c	c	c	c	c	c	c	c	c	c	c		c	c	**0.002**	34	c	c	c	c	c	c	c	c			c	c	c	c	c	0.013

Understorey species, d.b.h. > 5 cm — Distance *t* (m)

Plots	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	P
Mature 1	108	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Mature 2	463	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Logged 1	202	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Logged 2	277	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Landslide 1	324	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	**0.001**
Landslide 2	61	c	c	c	c	c	c	c	c	c	c						**0.001**

*c, Significant clumped distribution at distance *t* based on *L(t)*-function values distribution. An empty cell indicates random distribution (=, not applicable).

†Significance using 99% confidence interval (99 simulations) with a 1-m step. The Cramer–von Mises test was used for overall significance of patterns over the complete range of *t*. Bold type, spatial dispersion highly significant at 0.01 level.

The predominant companion species were *G. avellana* and *C. alba*, which exhibited negative spatial associations with all size classes of *N. glauca* ($P < 0.01$; Table 6) at mature site plot 2, logged site plot 1 and landslide site plot 1 (*G. avellana*), and mature site plot 2 (*C. alba*). At mature site plot 1 we found that the bamboo species *C. cumingii* was negatively associated with saplings of *N. glauca* only ($P < 0.01$; Table 6), while *P. mucronata* was negatively associated with adult trees of *N. glauca* ($P < 0.01$), but not with saplings. We also found that saplings of *G. avellana* were positively associated with adult trees of *N. glauca* ($P < 0.01$), but negatively associated with its saplings ($P < 0.01$). At mature site plot 2, the spatial association of *C. cumingii* was negative when compared with *N. glauca* trees of 5–15 cm d.b.h. and saplings at all distances ($P < 0.01$; Table 6), but positive in the first 6 m when compared with adult trees > 15 cm d.b.h. ($P < 0.01$). Finally,

at landslide site plot 2, we found that *L. caustica* had a negative spatial association with *N. glauca* saplings ($P < 0.01$), having an independent association with adult trees of *N. glauca* ($P > 0.05$; Table 6).

DISCUSSION

Like many other mesophytic temperate forest ecosystems, *Nothofagus* forests in southern Chile are often products of large disturbance events, including landslides, mudslides, windstorms and fire (Veblen & Ashton, 1978; Veblen *et al.*, 1996; Pollmann & Veblen, 2004). By contrast, some *Nothofagus* species (e.g. *N. antarctica*, *N. nitida*, *N. pumilio*) located in harsh habitats, subalpine or wet microsites tend to exhibit greater adaptations towards gap replacement (Rebertus & Veblen, 1993; Fajardo & de Graaf, 2004; Gutiérrez *et al.*, 2004).

Table 6 Patterns of specific spatial association based on the bivariate $L_{1,2}$-function between *Nothofagus glauca* (*N.g.*) size classes and species through all the study sites in Bullileo sector, San Fabián de Alico, Chile

Site	n_1/n_2	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	P
Mature 1																	
N.g. > 15 vs. *N.g.* saplings	33/244			−						−	−			−			0.024
N.g. 5–15 vs. *N.g.* saplings	65/244									−	−						0.053
N.g. > 15 vs. *Chusquea cumingii*	33/38		+			+	+										0.339
N.g. > 15 vs. *Pernettya mucronata*	33/70	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	**0.001**
N.g. > 15 vs. *Gevuina avellana*	33/49	+	+	+	+	+	+	+	+	+	+	+	+	+			**0.002**
N.g. > 15 vs. *Cryptocaria alba*	33/92																0.768
N.g. 5–15 vs. *C. cumingii*	65/38																0.888
N.g. 5–15 vs. *P. mucronata*	65/70	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	**0.001**
N.g. 5–15 vs. *G. avellana*	65/49	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**0.001**
N.g. 5–15 vs. *C. alba*	65/92																0.076
N.g. saplings vs. *C. cumingii*	244/38	−	−	−	−	−	−	−	−	−							**0.009**
N.g. saplings vs. *P. mucronata*	244/70													+	+	+	0.011
N.g. saplings vs. *G. avellana*	244/49			−	−	−	−	−	−	−	−	−	−	−	−	−	**0.001**
N.g. saplings vs. *C. alba*	244/92	+	+														0.295
Mature 2																	
N.g. > 15 vs. *N.g.* saplings	23/131													+	+	+	**0.007**
N.g. 5–15 vs. *N.g.* saplings	78/131	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**0.001**
N.g. > 15 vs. *Nothofagus obliqua*	23/15																0.506
N.g. > 15 vs. *Nothofagus leoni*	23/16				−								+				0.283
N.g. > 15 vs. *C. cumingii*	23/416	+	+	+	+	+	+										**0.001**
N.g. > 15 vs. *G. avellana*	23/87	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	**0.001**
N.g. > 15 vs. *C. alba*	23/42				−	−	−	−	−	−	−	−	−	−	−	−	**0.001**
N.g. 5–15 vs. *N. obliqua*	78/15																0.460
N.g. 5–15 vs. *N. leoni*	78/16																0.515
N.g. 5–15 vs. *C. cumingii*	78/416	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	**0.001**
N.g. 5–15 vs. *G. avellana*	78/87				−	−	−	−	−	−	−	−	−	−	−	−	**0.001**
N.g. 5–15 vs. *C. alba*	78/42	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	**0.001**
N.g. saplings vs. *N. obliqua*	131/15																0.726
N.g. saplings vs. *N. leoni*	131/16																0.585
N.g. saplings vs. *C. cumingii*	131/416	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	**0.001**
N.g. saplings vs. *G. avellana*	131/87	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	**0.001**
N.g. saplings vs. *C. alba*	131/42	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	**0.001**
Logged 1																	
N.g. > 15 vs. *N.g.* saplings	87/83									+	+	+	+	+	+	+	**0.002**
N.g. 5–15 vs. *N.g.* saplings	325/83	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**0.001**
N.g. > 15 vs. *G. avellana*	87/45	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	**0.004**
N.g. 5–15 vs. *G. avellana*	325/45	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	0.012
N.g. saplings vs. *G. avellana*	83/45	−	−	−	−					−	−	−	−	−	−	−	0.020
Logged 2																	
N.g. 5–15 vs. *N.g.* saplings	254/310	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**0.001**
N.g. 5–15 vs. understorey	254/324	+	+	+	+	+	+										0.093
Landslide 1																	
N.g. > 15 vs. *N.g.* saplings	53/70													+	+	+	**0.002**
N.g. 5–15 vs. *N.g.* saplings	104/70	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**0.001**
N.g. > 15 vs. *G. avellana*	53/26				−		−						−	−	−	−	0.412
N.g. 5–15 vs. *G. avellana*	104/26	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	**0.001**
N.g. saplings vs. *G. avellana*	70/26	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	**0.001**
Landslide 2																	
N.g. > 15 vs. *N.g.* saplings	31/34										+	+	+	+	+	+	**0.003**
N.g. 5–15 vs. *N.g.* saplings	102/34	+	+														0.246
N.g. > 15 vs. *Lithraea caustica*	31/56																0.056

Table 6 *continued*

Site	n_1/n_2	Distance, t (m)															P
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
N.g. 5–15 vs. *L. caustica*	102/56																0.944
N.g. saplings vs. *L. caustica*	36/56					−	−	−	−								**0.004**

+, Significant positive association; − significant negative association at distance t, based on $L_{1,2}(t)$-function. An empty cell indicates independent association. Significance using 99% confidence interval (99 simulations) with a 1-m step. The Cramer–von Mises test was used for overall significance of patterns over the complete range of t. Bold type, spatial association highly significant at 0.01 level.

Nothofagus glauca-dominated forests, as reported here, develop in a distinctive manner since they typically retain open, patchy canopies even > 140 years following disturbance. *Nothofagus glauca* had population structures indicative of continual recruitment across our oldest study site, constituting a steady-state population (Veblen, 1992). In addition, we found that the most diverse structure and species composition occurred in this oldest site. All these factors together suggest that *N. glauca*, even under good growing conditions, is growing in such a tough, moisture-limited environment that it is behaving like southern *Nothofagus* species growing on the most marginal of site conditions.

Mature stand: composition, structure and succession

While the mature site was sufficiently open to allow regeneration throughout the stand, it nevertheless showed a strong pattern of clumping of saplings. Various processes can lead to a clumped pattern of the youngest cohorts. For example, natural or mechanical soil disturbances may create patches of favourable seed bed; proximity to seed source or obstructions to seed movement, or patches of increased resource availability, which might be associated with canopy gaps (Veblen, 1992; Franklin et al., 2002). The pattern of sapling clumps in our sites is consistent with models of canopy-gap or patch-dynamics stand development (Pickett & White, 1985; Peet & Christensen, 1987).

Our oldest site had the most open canopy of our study sites (lowest LAI and highest percentage canopy-opening values), so that the presence of discrete gaps was rather difficult to define (Lieberman et al., 1989) and therefore might not be the principal cause of regeneration patchiness. Regarding the other processes, proximity to seed sources (seed shadow) might be a plausible cause for regeneration clumpiness, since seeds of this species appear to have limited mobility (largest seed size in the genus, 2000 seeds kg^{-1}; Donoso, 1996), therefore its dispersal can be confined to spots near parent trees. However, positive spatial associations between saplings and larger trees (> 15 cm d.b.h.) were not found, at least not at closer distances (< 10 m). The presence of *C. cumingii* might also play a role in regeneration patchiness, as it has been reported affecting the rate, timing and composition of tree regeneration in tree-fall gaps, particularly in southern Chile *Nothofagus* forests (González et al., 2002; Fajardo & de Graaf, 2004). The negative spatial association between *N. glauca* saplings and the bamboo species may reflect competition processes which have developed in niche differentiation displayed by the spatial patterns observed. It is not clear, however, what the competition source would be. Further studies are needed on resource partitioning and niche differentiation between *N. glauca* regeneration and *C. cumingii*, since these bamboos can become a threat to successful regeneration in *Nothofagus* forests (Veblen et al., 1996; González et al., 2002).

Mature stands of *N. glauca* have been reported to have open canopies with large gaps, which may explain their rich and diverse multilayered understorey (Amigo et al., 2000). Companion species, particularly shade-tolerant species, were more abundant in this site than in the rest. The presence of *C. alba*, a shade-tolerant species (Chacón & Bustamante, 2001), as well as *Persea lingue* and *Aextoxicum punctatum*, and the facultative shade-tolerant *G. avellana* (Figueroa & Lusk, 2001), may suggest some shift from shade-intolerant to shade-tolerant tree species dominance. Studies in mixed forests have shown that shade-intolerant *Nothofagus* species do not regenerate in undisturbed old-growth forests (Veblen et al., 1981; Pollmann, 2002). Nonetheless, along with what Pollmann (2002) has already suggested for *Nothofagus alpina*, the presence of tree-fall gaps (with reduced competitive effects) in general, along with increased light levels (high canopy openings) in particular for this study site, may be responsible for the continuous recruitment of *N. glauca*. On the other hand, there was not a clear spatial pattern when these species were compared with *N. glauca* size classes: positive in mature site plot 1 for *G. avellana*; and a negative association in mature site plot 2 for *G. avellana* and *C. alba*. These spatial patterns may be indicative of a mix of ecological factors influencing these patterns, including species ecological tolerance, historical factors and/or biotic interactions.

The spatial pattern established for *N. glauca* trees appeared to shift from a clumped to a random distribution with increases in size (hence age). This pattern is consistent with the interpretation that stand development consists of episodic tree establishment in small groups, followed by self-thinning (Peet & Christensen, 1987). This pattern is in accordance with what Fajardo & de Graaf (2004) reported for *N. pumilio* stands in two different localities of southern Chile, and for many other temperate forests around the world (Kenkel, 1988; Read & Hill, 1988; Stoll et al., 1994; Mast & Veblen, 1999). The large variety

of horizontal and vertical structures within the stand is also consistent with a history of continuous recruitment.

Effects of disturbances on stand structure and dynamics

In our logged site, it is clear that *N. glauca* is following a catastrophic regeneration mode with vigorous young trees of similar age showing evidence of competitive interactions and lower rates of regeneration (Veblen, 1992; Oliver & Larson, 1996). Human disturbances in *N. glauca* stands have been occurring primarily in the form of clearing forest patches of 1–3 ha. The timber is cut for charcoal, and debris is burned (locally called *roce*). Later, the site is abandoned and forest succession proceeds. If logging has not created serious soil disturbances, *N. glauca* vigorously resprouts from stumps (Donoso, 1993) and forms a dense, evenly aged second-growth stand. The sprouting nature might be the explanation for a significant clumped distribution among the size classes of *N. glauca* at this site.

Historically speaking, this disturbance–regeneration model is the one applicable to our study site. Litton & Santelices (2002) have also corroborated the disturbance–regeneration model for the Coastal range. However, San Martín & Donoso (1997) noted that anthropogenic degradation of *N. glauca* in the Coastal range can produce local shifts to dominance by sclerophyllous species, and more severe disturbances have resulted in invasions by exotic shrubs that often prevent forest regeneration. An intriguing, but as yet untested, hypothesis is that these disparate responses to human disturbance might be influenced by the size and degree of fragmentation of the landscapes within which these stands occur (perhaps, at larger scale, between the Coastal and Andean ranges).

Our landslide study site provides an interesting contrast in response to disturbance since, although older than our logged site, it sill represents an early successional state and a stem-initiation stand-development phase, after Oliver's model (Oliver & Larson, 1996). It also followed a catastrophic regeneration mode (Veblen, 1992), where *N. glauca* is the dominant species and there is continuous recruitment. Hence the particular nature and intensity of the disturbance make this site appear structurally different from the logged site. The LAI and BA are much lower than in the logged site. These stand characteristics, along with the presence of extremely rocky soil (pers. obs.), allow us to predict a low stand productivity. The landslide occurred in 1936, and since then there have been pulses of regeneration of *N. glauca*, followed by other shade-intolerant sclerophyllous species such as *Lithraea caustica* (Anacardiaceae) and *Lomatia hirsuta* (Proteaceae). All these characteristics provide evidence that *N. glauca* is a pioneer and a shade-intolerant tree species. A prompt colonization of *Nothofagus* species after catastrophic disturbances has commonly been reported to occur in southern Chile and Argentina, including *N. alpina* in the Malleco province (Pollmann, 2002) and *N. pumilio* in Tierra del Fuego (Rebertus & Veblen, 1993). *Nothofagus glauca* has many unique morphological adaptations to help deal with high temperatures and droughty soils in these extreme environments, including thick bark and tough, coriaceous leaves (Donoso, 1996; Ramírez *et al.*, 1997), which give an advantage over other *Nothofagus* species in the area (*N. obliqua*).

Saplings were mainly associated with adult trees, and the harsh characteristics of the site may account for this, even though *N. glauca* is a shade-intolerant tree species. In this moisture-limited site we might expect to see a reduced spatial association between regeneration and canopy openings, since canopy openings might be less hospitable to new germinants because of excessive temperatures and moisture stress. Some authors have argued that on more xeric habitats, reduced moisture stress under adult tree canopies may explain the increased sapling abundance beneath their canopies (Callaway, 1992; Bertness & Callaway, 1994). This positive spatial association may result from a facilitative relationship of larger 'nurse plants' providing shelter to seedlings by buffering physical stresses, especially high temperature. Bertness & Callaway (1994) suggested that facilitation could potentially play a more important role than competition in resource-limited environments.

CONCLUSIONS

Compared with other studies on dense *Nothofagus* rain forests in southern Chile, our study suggests that the regeneration of *N. glauca* is not necessarily dependent on large disturbances. Low canopy density allowed for diverse understorey species in all sites. These findings support the model of *Nothofagus* regeneration dynamics, which states that *Nothofagus* species occur in sites experiencing coarse-scale disturbances and/or in harsh conditions (for its potential competitors). *Nothofagus glauca* can be both a pioneer on harsh sites, and a gap strategist in mature forests. In these harsh sites the most species, the densest canopies and the most diverse structures occur in the oldest forests.

According to Amigo *et al.* (2000), the sites under study belong to the *Bomareo–Nothofagetum glaucae* phytosociological association. In this association *N. glauca* is the dominant tree species, and the presence of companion tree species will depend on the water-availability status of the area (Donoso, 1996). We found that *N. glauca* occurred with some tree species belonging to the mediterranean sclerophyll forest, such as *C. alba*, *L. caustica* and *Q. saponaria* (landslide site), but also found *N. glauca* accompanied by tree species more characteristic of southern Chilean rain forest, such as *A. punctatum* (mature site). The wide variety of plant associations in a small geographical area provides evidence as to the transitional nature of vegetation character in this zone (San Martín & Donoso, 1997).

The BA and density values differed according to site, due to different stand development stages. Maximum BA values were found in the second-growth stand following logging (logged site plot 1, 37.8 m^2 ha^{-1}) and in the mature stands (mature site plot 1, 33.1 m^2 ha^{-1}). *Nothofagus glauca* has lower BA

values when compared with other *Nothofagus* species of southern Chile: Pollmann (2002), working in Malleco Province (38°13′ S), found maximum BA values of 110 m^2 ha^{-1} for *N. alpina*. In old-growth stands of *N. pumilio*, Fajardo & de Graaf (2004) found BA values of 68 and 61.9 m^2 ha^{-1} in sites located in Ñuble Province (36°60′ S) and Coyhaique Province (45°52′ S), respectively. Our data suggest that the productivity levels of our *N. glauca* stands are well below those of *Nothofagus* species located in southern Chile. We suggest that mediterranean climatic conditions, characterized by long droughts plus thin, rocky soils (in the current study), in contrast to wet climates in the south, explain these low productivity rates (Kalin-Arroyo *et al.*, 1995; Mooney *et al.*, 2001).

The current study gives preliminary information on this particular *Nothofagus* forest type. Further studies on the links between regeneration behaviour, primary productivity, nutrient cycle and ecophysiology for these three stands are needed (Veblen *et al.*, 1996). Another important field of study to explore is the landscape connectivity that these Andean foothills share with the fragmented forests of the Coastal range.

Finally, extensive stand degradation and decreasing range size are serious concerns for *N. glauca*. Based on our work here, effective conservation of this species must include an understanding of both the landscape context and the spatial pattern of associated species.

ACKNOWLEDGEMENTS

REFERENCES

Amigo, J. & Ramírez, C. (1998) A bioclimatic classification of Chile: woodland communities in the temperate zone. *Plant Ecology*, **136**, 9–26.

Amigo, J., San Martín, J. & García Quintanilla, L. (2000) Estudio fitosociológico de los bosques de *Nothofagus glauca* (Phil.) Krasser del centro-sur de Chile. *Phytocoenologia*, **30**, 193–221.

Benoit, I. (1989) *El Libro Rojo de la Flora Terrestre de Chile*. CONAF, Santiago, Chile.

Bertness, M.D. & Callaway, R.M. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 187–191.

Bessag, J. (1977) Contribution to the discussion of Dr Ripley's paper. *Journal of the Royal Statistical Society, Series B*, **39**, 193–195.

Cale, W.G., Henebry, G.M. & Yeakly, J.A. (1989) Inferring process from pattern in natural communities. *Bioscience*, **39**, 600–606.

Callaway, R.M. (1992) Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. *Ecology*, **73**, 2118–2128.

Chacón, P. & Bustamante, R. (2001) The effects of seed size and pericarp on seedling recruitment and biomass in *Cryptocarya alba* (Lauraceae) under two contrasting moisture regimes. *Plant Ecology*, **152**, 137–144.

Cressie, N.A.C. (1993) *Statistics for spatial data*. Wiley, New York.

Dixon, P. (2002) Ripley's *K*-function. *The encyclopedia of environmetrics* (ed. by A.H. El-Shaarawi and W.W. Piergorsch), pp. 1796–1803. John Wiley & Sons, New York.

Donoso, C. (1993) *Bosques Templados de Chile y Argentina: Variación, Estructura y Dinámica*. Ecología Forestal Editorial Universitaria, Santiago, Chile.

Donoso, C. (1996). Ecology of *Nothofagus* forests in Central Chile. *The ecology and biogeography of* Nothofagus *forests* (ed. by T.T. Veblen, R.S. Hill and J. Read), 271–292. Yale University Press, New Haven, CT, USA.

Donoso, C., Grez, R., Escobar, B. & Real, P. (1984) Estructura y dinámica de bosques del tipo forestal siempreverde en un sector de Chiloé insular. *Bosque*, **5**, 82–104.

Duncan, R.P. (1989) An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrycarpus dacrydioides*). *New Zealand Natural Science*, **16**, 31–37.

Fajardo, A. & de Graaf, R. (2004) Tree dynamics in canopy gaps in old-growth forests of *Nothofagus pumilio* in Southern Chile. *Plant Ecology*, **173**, 95–106.

Figueroa, J.A. & Lusk, C.H. (2001) Germination requirements and seedling shade tolerance are not correlated in a Chilean temperate rain forest. *New Phytologist*, **152**, 483–489.

Ford, E.D. & Sorrensen, K.A. (1992). Theory and models of inter-plant competition as a spatial process. *Individual-based models in ecology: populations, communities and ecosystems* (ed. by D. DeAngelis and L. Gross), pp. 363–407. Chapman & Hall, New York.

Franklin, J.F., Spies, T.A., van Pelt, R., Carey, A.B., Thorburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K. & Chen, J. (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management*, **155**, 399–423.

Frazer, G.W., Canham, C.D. & Lertzman, K.P. (2000) GAP LIGHT ANALYZER (GLA), version 2.0: image processing software to analyze true-colour, hemispherical canopy photographs. *Bulletin of the Ecological Society of America*, **81**, 191–197.

González, M.E., Veblen, T.T., Donoso, C. & Valeria, L. (2002) Tree regeneration responses in a lowland

Nothofagus-dominated forest after bamboo dieback in South-Central Chile. *Plant Ecology*, **161**, 59–73.

Goreaud, F. & Pélissier, R. (2003) Avoiding misinterpretation of biotic interactions with the intertype *K*12-function: population independence vs. random labeling hypotheses. *Journal of Vegetation Science*, **14**, 681–692.

Gutiérrez, E., Armesto, J.J. & Aravena, J.C. (2004) Disturbance and regeneration dynamics of an old-growth North Patagonian rain forest in Chiloé Island, Chile. *Journal of Ecology*, **92**, 598–608.

Haase, P. (1995) Spatial pattern analysis in ecology based on Ripley's *K*-function: introduction and methods of edge correction. *Journal of Vegetation Science*, **6**, 575–582.

Haase, P. (2002) SPPA.EXE Statistical Program http://haasep. homepage.t-online.de.

Kalin-Arroyo, M.T., Zedler, P.H. & Fox, M.D. (eds) (1995) *Ecology and biogeography of Mediterranean ecosystems in Chile, California, and Australia*. Springer-Verlag, New York.

Kenkel, N.C. (1988) Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology*, **69**, 1017–1024.

Lieberman, M., Lieberman, D. & Peralta, R. (1989) Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology*, **70**, 550–552.

Liebhold, A.M. & Gurevitch, J. (2002) Integrating the statistical analysis of spatial data ecology. *Ecography*, **25**, 553–557.

Litton, C. & Santelices, R. (1996) Comparación de las comunidades vegetales en bosques de *Nothofagus glauca* (Phil.) Krasser en la Séptima Región de Chile. *Bosque*, **17**, 77–86.

Litton, C. & Santelices, R. (2002) Early post-fire succession in a *Nothofagus glauca* forest in the Coastal Cordillera of south-central Chile. *International Journal of Wildland Fire*, **11**, 115–125.

Lorimer, C.G., Frelich, L.E. & Nordheim, E.V. (1988) Estimating gap origin probabilities for canopy trees. *Ecology*, **69**, 778–785.

Lotwick, C.G. & Silverman, B.W. (1982) Methods for analyzing spatial processes of several types of points. *Journal of the Royal Statistical Society, Series B, Methodological*, **44**, 406–413.

Marticorena, C. & Quezada, M. (1985) Catálogo de la flora vascular de Chile. *Gayana*, **42**, 1–157.

Mast, J.N. & Veblen, T.T. (1999) Tree spatial patterns and stand development along the pine–grassland ecotone in the Colorado Front Range. *Canadian Journal of Forest Research*, **29**, 575–584.

McCune, B. & Grace, J.B. (2002) *Analysis of ecological communities*. MjM Software Design, Glededen Beach, OR, USA.

Mooney, H.A., Arroyo, M.T.K., Bond, W.J., Canadell, J., Hobbs, R.J., Lavorel, S. & Neilson, R.P. (2001). Mediterranean-climate ecosystems. *Global biodiversity in a changing environment. Scenarios for the 21st century*, Vol. 152 (ed. by F.S. Chapin III, O.E. Sala and E. Huber-Sannwald), pp. 157–200. Springer-Verlag, New York.

Oliver, C.D. & Larson, B.C. (1996) *Forest stand dynamics*. Wiley, New York.

Orwig, D.A., Cogbill, C.V., Foster, D.R. & O'Keefe, J.F. (2001) Variations in old-growth structure and definitions: forest dynamics on Wachusett Mountain, Massachusetts. *Ecological Applications*, **11**, 437–452.

Patterson, A.E. (1961) Distinguishing annual rings in diffuse porous tree species. *Journal of Forestry*, **59**, 126.

Peet, R.K. & Christensen, N.L. (1987) Competition and tree death. *BioScience*, **37**, 586–595.

Pickett, S.T.A. & White, P.S. (eds) (1985) *The ecology of natural disturbances and patch dynamics*. Academic Press, Orlando, FL, USA.

Pollmann, W. (2002) Effects of natural disturbance and selective logging on *Nothofagus* forests in south-central Chile. *Journal of Biogeography*, **29**, 955–970.

Pollmann, W. & Veblen, T.T. (2004) *Nothofagus* regeneration dynamics in South-central Chile: a test of a general model. *Ecological Monographs*, **74**, 615–634.

Ramírez, C., San Martín, J., Oyarzún, A. & Figueroa, H. (1997) Morpho-ecological study on the South American species of the genus *Nothofagus*. *Plant Ecology*, **130**, 101–109.

Read, J. & Hill, R.S. (1985) Photosynthetic response to light of Australian and Chilean species of *Nothofagus* and their relevance to the rain forest dynamics. *New Phytologist*, **101**, 731–742.

Read, J. & Hill, R.S. (1988) The dynamics of some rainforest associations in Tasmania. *Journal of Ecology*, **76**, 558–584.

Rebertus, A.J. & Veblen, T.T. (1993) Structure and tree-fall gap dynamics of old-growth *Nothofagus* forests in Tierra del Fuego, Argentina. *Journal of Vegetation Science*, **4**, 641–654.

Ripley, B.D. (1977) Modeling spatial patterns. *Journal of the Royal Statistical Society, Series B*, **39**, 172–212.

San Martín, J. & Donoso, C. (1997). Estructura florística e impacto antrópico en el bosque maulino de Chile. *Ecología de los Bosques Nativos de Chile* (ed. by J.J. Armesto, C. Villagrán and M.T.K. Arroyo), pp. 153–168. Editorial Universitaria, Santiago, Chile.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry. The principles and practice of statistics in biology research*, 3rd edn. W.H. Freeman, New York.

SPSS (2000) SYSTAT. SPSS Inc., Chicago, IL, USA.

Staudhammer, C.L. & LeMav, V.M. (2001) Introduction and evaluation of possible indices of stand structural diversity. *Canadian Journal of Forest Research*, **31**, 1105–1115.

Stoll, P., Weiner, J. & Schmid, B. (1994) Growth variation in a naturally established population of *Pinus sylvestris*. *Ecology*, **75**, 660–670.

Tilman, D. & Kareiva, P. (1997) *Spatial ecology. The role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, NJ, USA.

Veblen, T.T. (1985) Forest development in tree-fall gaps in the temperate rain forests of Chile. *National Geographic Research*, **1**, 162–183.

Veblen, T.T. (1992). Regeneration dynamics. *Plant succession: theory and prediction*, Vol. 11 (ed. by D.C. Glen-Lewin, R.K. Peet and T.T. Veblen), pp. 135–145. Chapman & Hall, London/New York.

Veblen, T.T. & Ashton, D.H. (1978) Catastrophic influences on the vegetation on the Valdivian Andes. *Vegetatio*, **36**, 149–167.

Veblen, T.T., Donoso, C., Schlegel, F.M. & Escobar, B. (1981) Forest dynamics in South-central Chile. *Journal of Biogeography*, **8**, 211–247.

Veblen, T.T., Donoso, C., Kitzberger, T. & Rebertus, A. (1996). Ecology of Southern Chilean and Argentinean *Nothofagus* forests. *The ecology and biogeography of Nothofagus* forests (ed. by T.T. Veblen, R.S. Hill and J. Read), pp. 293–353. Yale University Press, New Haven, CT, USA.

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Editor: Malte Ebach