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Mixed *Nothofagus* forest management: a crucial link between regeneration, site and microsite conditions

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Abstract

Canopy openings due to harvesting practices constitute a disturbance that changes the environmental conditions of microsites. Its impact on the relative performance of the regeneration of different tree species could also be affected by site conditions and forest structure. The objective of this study was to determine how regeneration establishment of *Nothofagus* mixed forests is influenced by shelterwood silvicultural system. We focused on Lanín National Reserve (Neuquén, Argentina) where this silvicultural system has been applied since the late 1980s. The microsite scale analysis (one managed forest) showed that canopy cover was a key factor conditioning *Nothofagus* regeneration establishment, with older and larger individuals growing in less exposed microsites. Low understory dominance and leaf litter thickness were also associated with microsites with regeneration, while successful establishment (saplings taller than 2 m) showed positive correlation with soil moisture. Variations of these patterns were observed among species reflecting their specific ecophysiological requirements. On a stand scale (two managed forests along Lacar watershed) regeneration of *N. dombeyi* and *N. alpina* showed significant correlation with site and specific basal area, while *N. obliqua* was correlated with total basal area. Regeneration taller than 2 m was mainly correlated with site and altitude. At both, microsite and stand scale, the relative abundance of species changed between mature trees and regeneration. In particular, for *N. alpina*, an abundance decrease was observed on regeneration. Our results suggest that forest management systems should diversify silvicultural practices throughout the forest landscape, to provide at each site the micro-environmental conditions required by each species in order to maintain biodiversity and forest functions.

Keywords Silvicultural prescriptions · Regeneration · Species composition · Mixed forest · Micro-environmental conditions · Canopy cover

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Introduction

Harvesting practices constitute a disturbance that changes the environmental conditions of microsites with possible effects on the relative performance of seedlings of different tree species and on the development of other understory species (Dezzotti et al. 2003; Wagner et al. 2011; Stuiver et al. 2016; Soto and Puettmann 2018). Therefore, in managed mixed forests and on a microsite scale, canopy openings (by changing light conditions, temperature and humidity of the soil and the amount of organic matter) could influence the spatial distribution of species, seedling establishment moment (early or late seral tree species) and their dominance in certain microsites (Silvertown 2004; Wagner et al. 2011). On a regional scale, ecosystems develop in a way that is extremely specific to site conditions (Weetman 1996). There is evidence of regeneration failures, despite application of recommended practices, for not taking into account ecosystem differences affecting regeneration and making adjustments to the prescription (Dey et al. 2009, Lopez Bernal et al. 2012). Therefore, forest management must consider not only natural regeneration dynamics but also possible interactions between site conditions (e.g. precipitation, temperature, altitude, soil type), forest structure (e.g. mature or immature forests, species proportions) and silvicultural systems (Weetman 1996). As seedling establishment is an indicator of forest management success (Wiser et al. 2007), understanding the effects of management on regeneration establishment (on microsite and stand scales) is crucial to the identification of appropriate forest practices (Wagner et al. 2018).

Nothofagus dombeyi (Mirb.) Oerst. (coihue), *Nothofagus alpina* [=*N. nervosa* (Poepp. et Endl.)] Oerst. (raulí) and *Nothofagus obliqua* (Mirb.) Oerst. (roble pellín) (Nothofagaceae) are ecologically and economically relevant tree species that produce high-quality timber in temperate regions of South America (Donoso 1993). Throughout their distribution, *N. obliqua* occurs mainly at a lower mean altitude (650–800 m.a.s.l.) than *N. alpina* (850–1350 m.a.s.l.) and *N. dombeyi* (650–2000 m.a.s.l.) but at intermediate altitudes (800–950 m.a.s.l.) these species coexist (Donoso et al. 2004). *Nothofagus* species re-colonize open sites and develop even-aged populations following the occurrence of natural large-scale disturbances (e.g., fire, earthquake, avalanche). In the absence of such events, small-scale perturbations (e.g., death of one or more mature trees creating small canopy gaps) produce environmental heterogeneity that promotes a forest with a mosaic of different ages (Veblen et al. 2004). In contrast to other *Nothofagus* forests (e.g. Chilean *Nothofagus* forests), in Argentina shade-tolerant competitor tree species (e.g. *Saxegothaea conspicua, Laureliopsis philippiana* and *Dasyphyllum diacantoides*) do not occur. Therefore, in these forests regeneration of *Nothofagus* species is not constrained by competition with shade tolerant tree species. Donoso (2006) reported, for example, that intolerant species such as *N. dombeyi* are able to regenerate even in small gaps in Argentina. However, *Chusquea culeou* bamboo, the dominant understory species, is particularly abundant in disturbed sites; and its abundant proliferation and considerable litter production could impair the colonisation and early development of *Nothofagus* (González et al. 2002; Giordano et al. 2009; Muñoz et al. 2012; Soto and Puettmann 2018).

Most of the natural distribution of these mixed *Nothofagus* forests is located within Lanín National Park (Sabatier et al. 2011), where different protection levels exist. Silvicultural management has been carried out within Lanín National Reserve administration (LNR) since the late 1980s, primarily using the shelterwood system. This system consists of successive regeneration cuttings (preparatory cuts in immature stands and seed cuts in mature stands) which retain partial forest cover (around 30–40%) until the regeneration phase is complete (approximately 20 years) (Chauchard et al. 1998, González Peñalba et al. 2010). The final cut, the last cut of the shelterwood system, has not yet been conducted in managed areas of LNR since the regeneration objective (2500 saplings/ha of more than 2 m height) has not been completely attained.

Despite decades of management of these forests, little is understood of the eco-physiological requirements of *Nothofagus,* and even less about how microsite heterogeneity caused by the shelterwood system influences regeneration establishment. Regarding eco-physiological requirements, it is known that these *Nothofagus* species have differences on shade tolerance (e.g. *N. alpina* being more tolerant than the others, Pollmann and Veblen 2004; Dezzotti 2008), the response to full-sun growth conditions (e.g. higher stomatal conductance for *N. obliqua* than for *N. alpina*, Varela et al. 2012) and the temperature of germination (e.g. lower for *N. alpina* than for *N. obliqua*, Arana et al. 2016). Considering management effects, modifications in the relative abundance of these species in post-harvest regeneration have been detected and related to changes in light conditions after management in a mixed forest (Sola et al. 2015). These data suggest that after management, microsite environmental conditions should selectively influence the regeneration pattern of *Nothofagus* species. Furthermore, taking into account that within LNR the shelterwood silvicultural system has been applied in areas different in site conditions (e.g. precipitation gradient) and forest structures (e.g. different species proportion), changes in patterns of regeneration establishment between areas are also expected.

The objective of this study was therefore to determine how regeneration establishment (e.g. presence, density, height and age of regeneration) of *Nothofagus* mixed forests is influenced by the shelterwood silvicultural system. On a microsite scale we focused on the influence of post-harvest microsite environmental conditions on the regeneration establishment of the three *Nothofagus* species. On a stand scale we focused on the influence of site, altitude and post-harvest forest structure on regeneration establishment of these species. Based on our results and previous research on these forests we finally presented proposals for management of *Nothofagus* mixed forests.

Materials and methods

Influence of post-harvest microsite environmental conditions on regeneration establishment (microsite scale)

We selected a study area located on Cerro Quilanlahue (40°8′S–71°28′W), at 930 m a.s.l., within Lanín National Reserve (LNR) (Neuquén, Argentina). This is an even-aged mixed stand composed entirely of *Nothofagus dombeyi*, *N. alpina* and *N. obliqua* (20, 44 and 36% respectively; Online Resource 1) with an understory dominated by *Chusquea culeou*. The area is on a north-aspect, lies across an elevation range of 40 m and the soils are classified as Andisols (Ferrer et al. 1991). The climate is humid temperate, with a mean annual temperature of 9 ºC and winter seasonality of precipitation (mean of 1800 mm/year, Autoridad Interjurisdiccional de Cuencas de los ríos Limay, Neuquén y Negro, AIC).

In 1993 a seed cut as part of a uniform shelterwood system was carried out at this site, reducing the canopy cover to 40% and maintaining the original relative composition of mature trees (Online Resource 1). Following this intervention, the site remained unmanaged. To evaluate the impact of microsite conditions on regeneration establishment we used a 2.85 ha rectangular plot established in 2009. This plot belongs to a network of Permanent

Plots for Genetics, Ecological and Management Studies (PPGEMS) and has previously been used to characterize the impact of management on the genetic diversity and species composition of mixed *Nothofagus* forest (Sola et al. 2015, 2016).

In 2013 we characterized post-harvest regeneration (individuals with root collar diameter < 10 cm and height < 4 m) in 80 sampling plots of 4 m^2 each (microsites), installed along 14 transects (~ 100 m) systematically distributed every 20 m (Online Resource 2). Six of these microsites fell on forest roads and therefore they were removed from the analysis. Height and number of individuals were recorder for each species of the remaining 74 microsites. Individuals taller than 2 m were considered as established regeneration, since they exceed the understory height and then they had low competition from understory species (Chauchard 1989). We measured six environmental variables for each of the 74 microsites: soil bulk density, soil moisture, soil temperature, leaf litter thickness, understory dominance and canopy cover.

Soil bulk density (SD) A steel cylinder of 125 cm^3, was inserted into the top of the mineral soil. The soil was removed from the cylinder and, once in the lab, oven-dried at 105 °C for 48 h to constant weight (dry weight) and weighed. Then, soil density was estimated as the dry weight divided by the volume of the sampling cylinder.

Soil moisture (SM) This was measured through the gravimetric method (i.e., weight difference between wet and dry soil) using the same soil samples collected for soil density estimation.

Soil temperature (ST) Measurements were performed with a thermometer placed at 5 cm depth (Sunlynn, precision of 0.1 °C) in soil points without the influence of sapling crowns. Measurements were taken at midday (during 1 h) in summer due to the importance of extreme temperatures with regard to drying and insolation.

Leaf litter thickness (LT) Soil pits were dug to measure litter thickness using a tape measure (precision of 1 mm).

SD, SM, ST and LT were determined at two randomly selected points of each microsite and their values were then averaged.

Understory dominance (UD) This was based on a semi-quantitative variable corresponding to the product of understory cover and average height (sensu Dezzotti et al. 2003). Understory cover represents the percentage of the sampling unit occupied by vertical projection of aerial parts of *Chusquea culeou,* the main understory species and the only one to compete with *Nothofagus* regeneration. Four categories were considered for understory cover: 0 (absence of understory), 1 (≤ 25%), 2 (25–50%) and 3 (≥ 50%). Understory average height was evaluated according to the categories 1 (< 30 cm), 2 (30–130 cm), and 3 (≥ 130 cm). Two categories of UD were then established: low dominance = 0, 1, 2 or 3 and high dominance = 4, 6 or 9.

Canopy cover (CC) This was determined by taking hemispherical photographs (Nikon D80, hemispherical, SIGMA 4.5 mm lens) from the center of each microsite, on cloudy days. The camera was placed on a tripod at a height of 1.2 m and oriented so that the top of each photograph pointed north. Canopy openness was calculated using Gap Light Analyzer 2.0 software (Frazer et al. 2000), which uses slope, exposure, zenith and altitude values for each plot, taking into account not only the canopy but also local topography. Openness was then transformed to cover. Although this variable was measured 20 years after harvesting, it could be used as proxy of canopy cover at the moment of management as Sola et al. (2015) reported that little reaction to management was detected for the remaining trees. When we found a microsite with regeneration taller than 1.2 m, hemispherical photographs were taken with some caution, in order to avoid the influence of regeneration in the cover measurement. When possible, saplings were pushed down, and in other cases the photographs were edited with the GAP Light Analyzer software to threshold the image so that each pixel was accurately classified as either a sky (white) or non-sky (black) pixel.

A correlation analysis procedure was applied to calculate correlations between pairs of quantitative variables using Statgraphics v. 15.2.06. Based on this, three uncorrelated quantitative variables (canopy cover, soil moisture, leaf litter thickness) were retained. Soil density was not included in the analysis as it was negatively correlated with soil moisture and leaf litter thickness, and soil temperature as it was negatively correlated with canopy cover (Online Resource 3). As the studied plot has a differential species distribution on mature trees across the slope (Online Resource 2), we added the categorical variable sub-plot (SP, lower and upper at 900 and 940 m a.s.l., respectively) in order to evaluate if species proportion on mature trees influences regeneration establishment.

We tested the effect of the variables on regeneration establishment considering: (1) the presence of regeneration (microsites with and without regeneration), (2) the presence of established regeneration (microsites with and without individuals > 2 m height), (3) the density of regeneration on each microsite and (4) the mean height of the regeneration of each microsite. For the variable density of regeneration natural log transformations were used to achieve normality. We used the logistic regression procedure for the first two analyses since the response variables were binary. We used generalized linear mixed models (GLMM) to test for the effect of the three uncorrelated quantitative variables, the categorical variable "understory dominance" (fixed factors) and the transects nested in sub-plots (random factor) on the density and height of the regeneration. Finally, we used the same GLMM to test for the effect of the variables on the age of each individual sapling, but we also included the categorical variable "species" as a fixed factor. Previously-adjusted height/age linear functions (Sola et al. 2015) were used for age estimations. A backward stepwise selection was applied for all analyses to find a parsimonious model that contained only statistically significant variables. It began with all variables in the model previously detailed and then variables were removed at a given step if their *p* values were greater than 0.05. Models were fit for total regeneration and for each species separately.

Influence of post-harvest forest structure and environmental conditions on regeneration establishment (stand scale)

We selected two sites of mixed *Nothofagus* forests of the LNR located along Lacar watershed (sites 1 and 2, Fig. 1), where management plans had recently been applied (Table 1). At these sites, silvicultural treatments were implemented in single-cohort stands with unimodal size distributions, and in the understory reinitiation and old-growth stages of forest development. Six and thirteen permanent plots were installed randomly after cuts in sites 1 and 2 respectively, and have been monitored over time. Regeneration was sampled in variable number of sub-plots systematically distributed in each permanent plot. Number of sub-plots and characteristics of forest structure, type of cut and summary statistics of harvest implemented in each permanent plot are summarized in Table 1. We analyzed monitoring data from these permanent plots to determine density (individuals/ha) and species composition of regeneration at a time with similar number of years after management (Table 1). Individual regeneration height was not available from monitoring data, however, recorded height categories (< 30 cm, 30–100 cm, 100–200 cm, 200–600 cm, > 600 cm) allowed us to discriminate total and established regeneration.

We used the logistic regression procedure and GLMMs to test for the effect of site, altitude and forest structure on regeneration establishment. Although mean annual

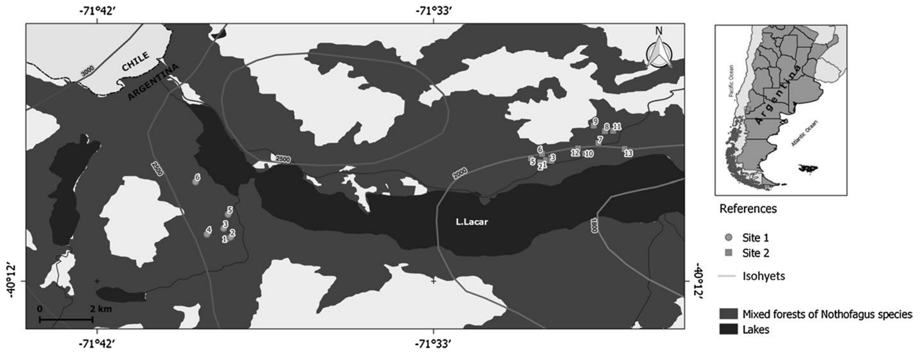

Fig. 1 Location of forest management plans in Lanín National Reserve. Color figure in Online Resource 5

precipitation level has an important variation along the Lacar watershed (Fig. 1), and it could be considered as a key factor influencing regeneration establishment, we cannot discard the influence of other unknown factors (e.g. soil type, temperature) on this process. Therefore, we considered site (1 and 2) as a factor for the analysis. Regarding forest structure, total basal area and density of mature trees (related to canopy cover) and basal area and density of each species (contemplating seed availability) were used. A correlation analysis procedure was applied to calculate correlations between pairs of these quantitative variables using Statgraphics v. 15.2.06. Based on this, only uncorrelated variables were retained for the analysis. For total regeneration (*Nothofagus* spp) total basal area and density were include, while for species level analyses, total basal area and density and basal area of each species were included. Density of each species was eliminated as it was correlated with total and/or species basal area (Online Resource 4). We tested the effect of variables on regeneration establishment considering: (1) the presence of regeneration (permanent sub-plots with and without regeneration), (2) the presence of established regeneration (permanent sub-plots with and without individuals > 2 m height) and (3) the density of regeneration on each permanent sub-plot. Natural log transformations were used to achieve normality of density of regeneration. Models were fit for total regeneration and for each species separately, using the regression procedure previously described for the local scale analyses. We used the logistic regression procedure for the first two analyses and GLMM for the third analysis to test for the effect of the site, altitude, uncorrelated forest structure variables (fixed factors) and the plots nested in sites (random factor) on the density of the regeneration.

Considering that for the plot studied on the microsite scale (Quilanlahue) a change in the specific composition between mature trees and post-harvest regeneration had previously been reported (Sola et al. 2015, 2016), the proportion of species in each stratum was also compared using contingency tables and Chi Square test. Comparisons were made at site level, averaging the regeneration density of the plots of each site.

Results

We summarize here the main results of the analyses. Range, mean and standard deviation of quantitative environmental variables are provided in Online Resource 7 and 8.

Table 1 Characteristics of permanent plots (size, forest development stage and number and size of sub-plots) and summary statistics of harvest implemented in the two sites of mixed *Nothofagus* forests of the Lanín National Reserve. Forest dynamic stages sensu Oliver and Larson 1996 (1, stand initiation; 2, stem exclusion; 3, understory reinitiation; 4, old-growth) were used to characterize development stage of plots. Table adapted from Chauchard (1989), Chauchard et al. (1998) and González Peñalba et al. (2010). Post-harvest density and post-harvest basal area of each species are included in Online Resource 6

Site	Plot	Size (m^2)	Forest development stage	No. of sub-plots	Size of each sub-plot (m^2)	Applied cut	Year of logging	Years from logging to evaluation	Post-harvest density (individuals/ha)	Post-harvest basal area (m^2/ha)
1	1	1000	3	4	4	Seed cut	1988	19	210	24
1	2	1000	3	4	4	Seed cut	1988	19	180	36
1	3	1000	3	4	4	Preparatory cut	1990	24	280	27
1	4	1000	4	4	4	Seed cut	1991	19	60	40
1	5	1000	3, 4	4	4	Seed cut	1993	21	80	21
1	6	1000	3, 4	4	4	Seed cut	1999	16	170	38
2	1	500	3, 4	8	1	Seed cut	1995	19	240	21
2	2	500	3, 4	8	1	Seed cut	1995	19	180	48
2	3	500	3, 4	8	1	Seed cut	1996	18	100	24
2	4	500	3, 4	8	1	Seed cut	1997	17	260	38
2	5	500	3	8	1	Preparatory cut	1998	16	280	37
2	6	500	3, 4	8	1	Seed cut	1999	15	200	28
2	7	2700	3, 4	4	12	Seed cut	1996	20	78	26
2	8	900	3, 4	4	4	Seed cut	1997	15	121	28
2	9	2000	3, 4	4	4	Seed cut	1998	17	245	24
2	10	2000	3, 4	4	4	Seed cut	1999	16	150	28
2	11	2700	3, 4	4	12	Seed cut	1995	17	148	25
2	12	1200	3, 4	4	4	Seed cut	2000	15	64	23
2	13	2000	3, 4	4	4	Seed cut	2001	15	110	30

Influence of post-harvest microsite environmental conditions on regeneration establishment (microsite scale)

Mean regeneration density was 12,751 individuals/ha, but a high level of variability was observed (standard error, SE = 23,048) among microsites. Species proportions were 44, 17 and 39% for *N. dombeyi, N. alpina* and *N. obliqua* respectively, with 35% of microsites showing no regeneration. Mean height was 1.52 m (SE = 1.42), which is lower than the 2 m threshold considered for established regeneration. The logistic regression analysis indicated that lower sub-plot, high understory dominance, canopy cover and leaf litter thickness had a significant effect on the presence of regeneration, explaining around 50% of the variation (Table 2). The effect of these factors on the presence of regeneration for each species was lower than for *Nothofagus* spp., and revealed a distinctive pattern in *N. dombeyi* regeneration respect to the other two species (Table 2).

Nothofagus established regeneration represented less than 1/3 of total regeneration (Fig. 2). Differences on its contribution were however observed among species, being lower for *N. alpina* than for *N. obliqua* and *N. dombeyi* (Kruskal–Wallis test $p < 0.05$) (Fig. 2). The logistic regression analysis revealed that canopy cover, soil moisture and leaf litter thickness had a significant effect on presence of established regeneration (taller than 2 m, Table 2). Analyzed factors explained a high proportion of the variation for *N. dombeyi* and *N. alpina*, but differences were observed for the significant factors between them (Table 2). Canopy cover and leaf litter thickness explained the variation of the presence of *N. dombeyi* established regeneration, while canopy cover and soil

Table 2 Parameter estimates of predictor variables including microsite environmental conditions of logistic regression models for the presence of regeneration and established regeneration, total and of each species (microsites with vs without saplings and; microsites with and without individuals > 2 m height)

Predictor	*Nothofagus* spp.	*N. dombeyi*	*N. alpina*	*N. obliqua*
Presence of regeneration				
R^2	57%***	15%***	19%***	22%***
Intercept	−10.11	−8.11	2.68	5.18
Canopy cover	0.32**	0.13*		
Leaf litter thickness	−1.07***		− 0.52*	−0.78***
Understory dominance (high)	−2.71**		−2.13**	−1.33*
Sub-plot (lower plot)	−3.62***	−1.37**		
Presence of established regeneration				
R^2	35%***	53%***	42%**	
Intercept	−22.36	−25.4	−28.26	
Soil moisture	0.11**		0.14*	
Canopy cover	0.38***	0.52***	0.31*	
Leaf litter thickness	−1.43***	−1.81***		

The coefficients of determination (R^2) and p values of the models are shown. *$p < 0.05$; **$p < 0.01$, ***$p < 0.001$. Only significant fixed effects for at least one analysis are reported. Empty cells denote that the effect was not included for being not significant in the specific analysis. The number of microsite evaluated for the presence of regeneration was 74 and for the presence of established regeneration was 51 for *Nothofagus* spp., 33 for *N. dombeyi*, 23 for *N. alpina* and 39 for *N. obliqua*

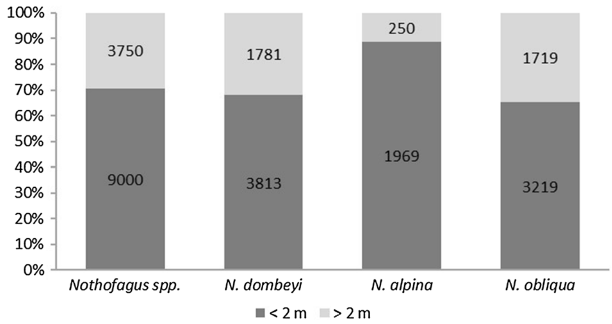

Fig. 2 Regeneration density (individuals/ha) of the three species (*Nothogafus* spp.), *N. dombeyi*, *N. alpina* and *N. obliqua* in two height-classes 20 years after the seed cut. Data from 74 microsites in Quilanlahue

moisture explained the variation of *N. alpina* regeneration. Surprisingly none of the tested factors explained the variation of established regeneration for *N. obliqua*.

The backward stepwise selection process applied for GLMM analyses reveals that only fixed factors influenced the response variables (Table 3). Leaf litter thickness and canopy cover were the variables associated with the density of regeneration of *Nothofagus* spp. and *N. dombeyi* and *N. alpina*, respectively. However, these factors explained less than 25% of the variation (Table 3). None of the tested factors explained the variation of density of regeneration for *N. obliqua*. For the mean height of regeneration canopy cover was a key factor for *Nothofagus* spp. and all three species; but species specific patterns related to soil moisture (*N. alpina*) and understory dominance (*N. obliqua*) were also observed (Table 3).

Finally, only canopy cover and species showed a significant effect on the age of the regeneration (Table 4), explaining 28% of the observed variation ($p<0.001$). *N. alpina* saplings were younger than those of *N. obliqua* and *N. dombeyi* (Fig. 3).

Table 3 Parameter estimates of predictor variables including microsite environmental conditions of generalized linear models for the density of regeneration and the mean height of regeneration (response variables)

Predictor	*Nothofagus* spp.	*N. dombeyi*	*N. alpina*	*N. obliqua*
Density of regeneration				
R^2	15%**	25%**	21%*	
Intercept	−3.34	3.23	6.93	
Soil moisture				
Canopy cover			−0.09*	
Leaf litter thickness	−0.34**	−0.39**		
Mean height of regeneration				
R^2	20%***	38%***	43%**	29%**
Intercept	−6.65	−8.45	−12.13	−3.51
Soil moisture			0.07*	
Canopy cover	0.12***	0.15***	0.15*	0.08*
Understory dominance				0.72*I1(1)**

The coefficients of determination (R^2) and *p* values of the models are shown. *$p<0.05$; **$p<0.01$; ***$p<0.001$. Only significant fixed effects for at least one analysis are reported. Empty cells denote that the effect was not included for being not significant in the specific analysis. The number of microsite evaluated for the density and mean height of regeneration was 51 for *Nothofagus* spp., 33 for *N. dombeyi*, 23 for *N. alpina* and 39 for *N. obliqua*. I1(1) = 1 if understory dominance = high, − 1 if understory dominance = low

Table 4 Parameter estimates of predictor variables including microsite environmental conditions of generalized linear models for the age of regeneration

Age of regeneration	
Intercept	− 17.33
Species	1.05*I1(1)–1.76*I1(2)***
Canopy cover	0.34***

Only significant fixed effects for at least one analysis are reported. *$p<0.05$; ***$p<0.001$. I1(1) = 1 if species = *N. dombeyi*, − 1 if species = *N. obliqua*, 0 otherwise; I1(2) = 1 if species = *N. alpina*, − 1 if species = *N. obliqua*, 0 otherwise. The number of individuals analyzed was 409

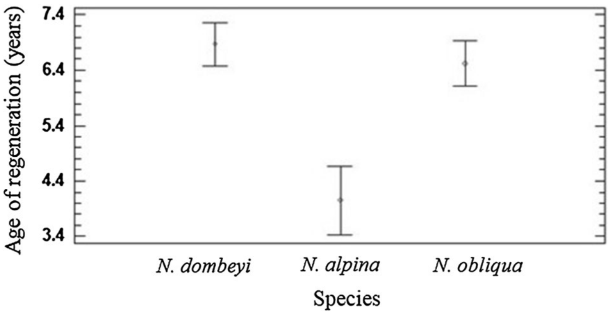

Fig. 3 Age of regeneration of *N. dombeyi*, *N. alpina* and *N. obliqua* 20 years after the seed cut in Quilanlahue

Influence of post-harvest forest structure and environmental conditions on regeneration establishment (stand scale)

Mean regeneration density was 53,021 and 4183 individuals/ha for site 1 and 2 respectively (85% higher in site 1 than in site 2), but a high level of variability was observed among sub-plots (SE = 82,382 and 6960 respectively). The logistic regression analysis indicated that site 1 had significant effect on the presence of *Nothofagus* spp, *N. dombeyi* and *N. alpina* regeneration (Table 5). In these two species the specific basal area of mature trees also contributed to explain the variation. On the other hand, tree total basal area had a significant effect on the presence of *N. obliqua* regeneration. With the exception of *N. alpina*, significant factors explained less than 15% of the variation (Table 5).

Nothofagus established regeneration represented around 25% of total regeneration in both sites (Fig. 4). However, differences were observed among species between sites (Fig. 4). The logistic regression analysis only revealed significant effects of site 1 and altitude on the presence of regeneration taller than 2 m of *N alpina* and *N. obliqua*. These factors explained more than 50% of the variation of these two species, but with opposite patterns (Table 5). Interestingly, none of the tested factors explained the variation of established regeneration of *Nothofagus* spp. and *N. dombeyi*.

The backward stepwise selection process applied for GLMM analyses reveals that only fixed factors influenced the density of regeneration (Table 6). Site had a significant effect on total density of *Nothofagus* spp. regeneration and on *N. alpina* regeneration along with altitude. While for *N. dombeyi* total basal area of mature trees influenced the density of regeneration. None of the tested factors explained the variation of density of regeneration for *N. obliqua*.

Table 5 Parameter estimates of predictor variables including site, altitude and post-harvest forest structure of the logistic regression models for the presence of regeneration and established regeneration

Predictor	*Nothofagus* spp.	*N. dombeyi*	*N. alpina*	*N. obliqua*
Presence of regeneration				
R^2	14%***	13%***	42%***	7%*
Intercept	1.03	−1.8	−4.65	1.18
Basal area of the species		0.04*	0.09**	
Total basal area				−0.12*
Site (1)	2.13***	1.63**	3.65***	
Presence of established regeneration				
R^2			63%**	54%**
Intercept			−33.52	607.99
Altitude			0.02*	−0.66**
Site (1)			19.91**	−197.98***

The coefficients of determination (R^2) and *p* values of the models are shown. *$p<0.05$; **$p<0.01$; ***$p<0.001$. Only significant fixed effects for at least one analysis are reported. Empty cells denote that the effect was not included for being not significant in the specific analysis. The number of sub-plots evaluated for the presence of regeneration was 104 and for the presence of established regeneration was 40 for *Nothofagus* spp., 29 for *N. dombeyi*, 15 for *N. alpina* and 11 for *N. obliqua*

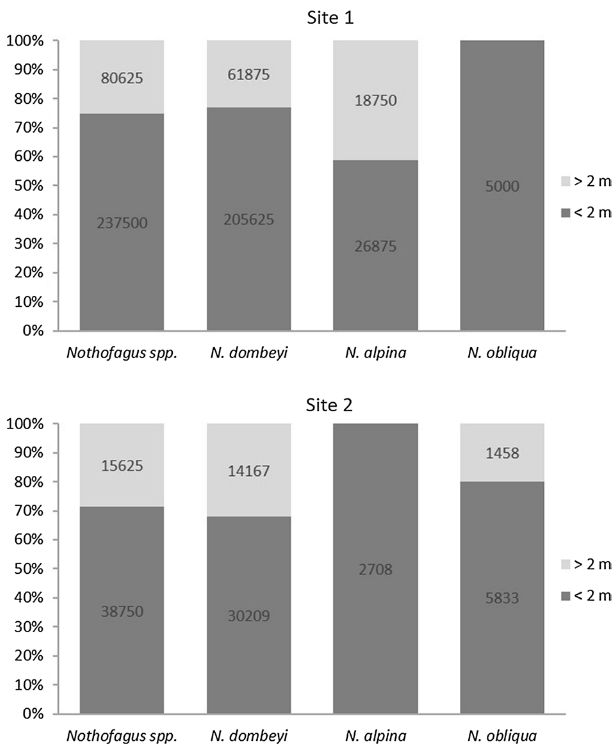

Fig. 4 Regeneration density (individuals/ha) of the three species (*Nothogafus* spp.), *N. dombeyi*, *N. alpina* and *N. obliqua* in two height-classes for the two sites of managed mixed *Nothofagus* forests of the Lanín National Reserve

Table 6 Parameter estimates of predictor variables including site, altitude and post-harvest forest structure of generalized linear models for the density of regeneration

Predictor	*Nothofagus* spp.	*N. dombeyi*	*N. alpina*	*N. obliqua*
Density of regeneration				
R^2	11%*	22%*	47%**	
Intercept	9.67	8.88	5.7	
Basal area of the species		0.05*		
Altitude			0.01*	
Site	0.46*I1(1)*		0.82*I1(1)**	

The coefficients of determination (R^2) and *p* values of the models are shown. *$p<0.05$; **$p<0.01$. Only significant fixed effects for at least one analysis are reported. The number of sub-plots analized was 40 for *Nothofagus* spp., 29 for *N. dombeyi*, 15 for *N. alpina* and 11 for *N. obliqua*. I1(1) = 1 if site = 1, − 1 if site = 2

A significant change of the relative abundance of species between mature trees and post-harvest regeneration was registered, with *N. dombeyi* showing significantly higher recruitment than *N. alpina* and *N. obliqua* in both sites (Site 1 $\chi^2 = 11{,}439.67$, $p<0.05$; Site 2 $\chi^2 = 1078.52$, $p<0.05$. $p<0.05$; Table 7). Within sites, differences in recruitment patterns were observed between plots at species level. In site 2, recruitment was mainly dominated by *N. dombeyi* individuals regardless of mature tree composition, but some plots showed *N. obliqua* dominance (Online Resource 9). *N. alpina* regeneration was not dominant in any plot, even though adult trees were present in the upper canopy of 70% of them (Online Resource 9). In site 1, *N. dombeyi* also represented an important percentage of the regeneration, but some plots showed *N. alpina* dominance (Online Resource 9). In these plots, the upper canopy was also dominated by *N. alpina* and most of these regeneration constituted advanced regeneration (pre-harvest).

Table 7 Relative abundance of species in mature trees and post-harvest regeneration in the two sites of mixed *Nothofagus* forests of the Lanín National Reserve. Adapted from Chauchard (1989), Chauchard et al. (1998) and González Peñalba et al. (2010)

Managed area	Species	Post-harvest mature trees % (individuals/ha)	Regeneration % (individuals/ha)
Site 1	*N. dombeyi*	20 (33)*	84 (44,583)*
	N. alpina	45 (73)*	14 (7604)*
	N. obliqua	35 (57)*	2 (833)*
	Total	100 (163)	100 (53,021)
Site 2	*N. dombeyi*	11 (19)*	82 (3414)*
	N. alpina	45 (75)*	5 (208)*
	N. obliqua	44 (73)*	13 (561)*
	Total	100 (167)	100 (4183)

Chi Square test, significant: *$p<0.05$

Discussion

Influence of post-harvest microsite environmental conditions on regeneration establishment

The microsite scale analysis showed that canopy cover was a key factor conditioning *Nothofagus* regeneration establishment, with older and larger individuals growing in less exposed microsites (higher canopy cover). This pattern may be related to the better performance of saplings of *Nothofagus* species growing in partial shade (Dezzotti et al. 2003; Varela et al. 2012; Donoso et al. 2015). It also agrees with previous reports on managed mixed *Nothofagus* forests where post-harvest regeneration was concentrated in patches along the edges of gaps (Dezzotti and Sbrancia 2006). Based on the correlation found between canopy cover and soil temperature (Online Resource 3), the influence of this variable could also be considered as an explanation for the detected pattern. However, we determined current soil temperature; therefore, extrapolations on its influence on regeneration establishment should be considered with caution. The influence of canopy cover on regeneration establishment has been previously reported for other forest tree species (e.g. Gallo 2015; Agestam et al. 2003), suggesting that forest regeneration may be improved by management of canopy density.

Low leaf litter thickness favored higher density and presence of established regeneration. This is probably because thick litter cover acts as a physical barrier constraining tree establishment in understories, especially for species with small seeds as those of *Nothofagus* spp. (González and Donoso 1999; Christie and Armesto 2003; Donoso 2006). On the other hand, low understory dominance favored regeneration (78% of microsites), probably reflecting reduced competition from understory species as has been previously reported (González et al. 2002; Giordano et al. 2009). However, the low proliferation of *C. culeou* in microsites with high canopy cover, previously reported (Veblen et al. 1996; Soto and Puettmann 2018) and also detected in our work (*t* test, $p<0.05$), could also explain this effect. The increase in understory species with increasing harvest intensity and the negative effect of litter on seedling establishment have been reported in several forests (Nilsson et al. 2006; Wagner et al. 2011; Gallo 2015; Stuiver et al. 2016). Thus, ground disturbance (e.g., slash, humus, or topsoil removal by scarification) has been recommended to manage competitive vegetation and encourage more reliable regeneration of desirable trees in a number of forest biomes (Veblen et al. 1996; Agestam et al. 2003; Yoshida et al. 2005; Reyes et al. 2014).

Some differences on the patterns were however detected among *Nothofagus* species. For example, *N. dombeyi* and *N. obliqua* regeneration was established first (mean ages of 7.1 and 6.5 years respectively); while *N. alpina* was the last species established (mean age 3.5 years). On the other hand, only for *N. alpina* saplings, soil moisture explained the presence of established regeneration; possibly indicating an early recruitment (or low early mortality) in humid microsites. However, extrapolations on its influence on *Nothofagus* regeneration dynamics should be considered with caution because we used a current measure of soil moisture. Contrary to expectations, higher density of *N. alpina* regeneration was found in microsites with low canopy cover, but these individuals were seedlings (mean height of 0.10 m, $SE=0.08$). This result highlight the importance of consider not only density as an indicator of successful regeneration as it could be a biased estimation, considering the low chance of their successful establishment. However, results could also indicate that *N. alpina* protection requirements are currently being achieved. Differences on seedling responses to post-harvest microsite conditions has been previously reported, highlighting the need to adapt any management procedure to match the specific requirements of the species of interest (e.g. Guay-Picard et al. 2015; Stuiver et al. 2016).

Influence of post-harvest forest structure and environmental conditions on regeneration establishment

The stand scale analysis showed that regeneration establishment differed with post-harvest forest structure and environmental conditions. Site was a key factor influencing the regeneration establishment. Globally, the success of regeneration establishment of *Nothofagus* spp. was higher for the site with higher mean annual precipitation, but differences were observed among species. The more humid site correlated mainly with regeneration establishment of *N. alpina* (all three regeneration response variables positively associated); while for *N. obliqua* only a negative correlation was detected for the presence of established regeneration. The more humid site also correlated with presence of regeneration of *N. dombeyi*, however this species constituted around 80% of the regeneration of both sites. These results agreed with previous reports of species occurrence such as: (1) *N. alpina* occurrence restricted to conditions of moderate water stress, whereas *N. obliqua* occurrence tolerate greater variation (Weinberger and Ramírez 2001), and (2) *N. dombeyi* occurrence along wide ecological amplitude, broad geographic range and on more variety of sites within the landscape (Veblen et al. 1996; Pollmann 2004).

Altitude was only significant at species level, being positively and negatively correlated with the establishment of *N. alpina* and *N. obliqua* regeneration, respectively. This result is in accordance with the natural altitudinal distribution of species (Donoso et al. 2004) and probably associated with the temperature of germination (which is lower for *N. alpina* than for *N. obliqua*, Arana et al. 2016). Post-harvest forest structure constituted a less significant effect. *N. dombeyi* regeneration was mainly associated with greater specific basal area suggesting a dependence on seed availability. Despite the greater production of seeds reported for this species compared to *N. obliqua* and *N. alpina* (Dezzotti et al. 2016), the dependence on seed availability could be explained for its low seed viability (mean value of 20% in years with high seed production, Burschel et al. 1976). Total basal area was only negatively correlated with presence of regeneration of *N. obliqua*. These results could be related to the species requirement of lower canopy cover to regenerate (around 40%, Weinberger and Ramirez 1999).

Influence of silviculture management on *Nothofagus* regeneration establishment

Successful regeneration is a critical part of sustainable forest management (Wiser et al. 2007; Wagner et al. 2018). Management plans for *Nothofagus* forests expected that recruitment began 5 years after logging and that regeneration establishment (2500 saplings/ha, taller than 2 m and homogeneously distributed) were successful after 10 years (Chauchard et al. 2012). However, after 20 years the regeneration objective was not successfully achieved in all study plots. Even more, both managed areas showed changes in species composition between mature trees and post-harvest regeneration. For that reason, we focused on the influence of shelterwood silvicultural system on the regeneration establishment of *Nothofagus* mixed forests, considering not only presence and density of regeneration but also mean height and age of regeneration and/or the presence of established regeneration (taller than 2 m) of each species to make a more comprehensive analysis of the process. Globally our results indicated that the influence of shelterwood system on *Nothofagus* regeneration varied with microsite and stand conditions. The pioneer and widely distributed species *N. dombeyi* has been favored in all managed areas, while *N. obliqua* was associated to low altitude and open microsites (reduced basal area of mature trees and low competition of understory species) and *N. alpina* was restricted to shady conditions with moderate water stress and high altitude.

Nothofagus alpina was the species under-represented in total regeneration; while previous studies revealed that it represented 92% of pre-harvest regeneration (regeneration established with closed canopy) (Sola et al. 2015). A similar trend of species composition change has also been reported after the implementation of the group selection cutting silvicultural system (Dezzotti et al. 2003). Weinberger and Ramirez (1999) showed that juvenile stages of *N. alpina* became established only in shady conditions (with cover > 40%) in sites with low precipitation levels. Thus, reproductive strategies do not depend only on light, but on the interaction with other environmental factors such as temperature and water economy, e.g. in low altitudes or in sites with low precipitation levels *N. alpina* could only regenerate in small gaps (Pollmann and Veblen 2004; Weinberger and Ramirez 1999, 2001). Therefore, management prescriptions for *Nothofagus* forests in Argentina should be revised considering interspecific differences in requirements and the interactions with site conditions, forest structure and silvicultural system.

Silvicultural management proposal for *Nothofagus* mixed forests

Interruption or changes in forest regeneration processes induced by human activities is prevalent in many places around the world (Kozlowski 2002). These problems range from a simple lack of regeneration to a shift in species composition, which is less desirable economically and ecologically. For this reason, alternative silviculture systems are being used in many forests (e.g. Paquette et al. 2006; Wiser et al. 2007; Guay-Picard et al. 2015; Stuiver et al. 2016). Based on our results and previously reported data, we propose an irregular shelterwood system to promote structural diversity while maintaining the simplicity of even-aged management. A first harvest of low intensity should be applied (residual canopy cover greater than 60%, especially in sites with more stressful conditions), to facilitate seedling establishment, with more favorable conditions for mid-tolerant to shade species; and then a second more intense cut, allowing the release of previously established regeneration. This sequence is expected to favor *N. alpina* establishment first and to prevent the rapid colonization of *Chusquea culeou*, and then, with larger canopy openings, to promote the establishment of a new cohort of the other *Nothofagus* species. This prescription, becomes even more relevant given the predictions of future climate scenarios, in which the distribution range of *N. alpina* would be drastically reduced (Marchelli et al. 2017). Finally, in mixed stands of the three species, a larger proportion of *N. dombeyi* individuals could be harvested, favoring higher seed availability of the other species, in order to maintain the original composition in the new generation.

On the other hand, in areas under management, where the *N. obliqua,* and mainly *N. alpina* regeneration processes are affected, the following recommendations should be taken into account. In sites with successful recruitment dominated by *N. dombeyi*, regeneration management of this species (thinning) should be implemented to promote the release of *N. obliqua* and *N. alpina* individuals. In sites without post-harvest regeneration or with low sapling density, topsoil removal and/or planting of the most affected species could be implemented considering previous reports (Soto and Puettmann 2018; Paquette et al.

2006). The feasibility of underplanting is promising considering published studies on seed production areas, crop, nursery and plantation of *Nothofagus* species (Gallo 1993; Donoso and Lara 1999; Azpilicueta et al. 2013; Donoso et al. 2013; Gallo 2013; Soto et al. 2015).

Conclusions

Based on our study we conclude that canopy cover after intervention is a key factor modelling regeneration dynamics in mixed forest (presence of regeneration, species composition, mean height and regeneration establishment moment), but other factors such as site conditions and forest structure are also relevant and should be taken into consideration. Management systems of mixed *Nothofagus* forests should, therefore, diversify silvicultural practices throughout the forest landscape, in order to provide the micro-environmental conditions required by each species and to maintain biodiversity and forest functions. Further research into landscape dynamics will be important to help make conservation decisions concerning areas, landscapes and species.

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