Alternative silvicultural practices with variable retention to improve understory plant diversity conservation in southern Patagonian forests

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ABSTRACT

Understory plants could can act as indicators of temperate forest sustainability, health and conservation status due to their importance in ecosystem function. Harvesting impacts on understory plant diversity depends on their intensity. Variable retention has been proposed to mitigate the harmful effects of timber harvesting, but its effectiveness remains unknown in southern Patagonian *Nothofagus pumilio* forests. The objectives of this study were to: (i) define a baseline of understory plant diversity in old-growth forests along a site quality gradient and under canopy gaps; (ii) evaluate stands with three different variable retention treatments compared to old-growth forests; and (iii) assess temporal changes during 4 years after harvesting (YAH). A 61 ha *N. pumilio* forest was selected. Understory plant (Dicotyledonae, Monocotyledonae and Pteridophyta) richness, cover (including woody debris and bare forest floor) and aboveground dry biomass were characterized in summer for 5 years. Before harvesting, baseline samples were conducted along a site quality gradient and outside/inside canopy gaps. Analyzed treatments include a control of old-growth forest (OGF) and three different harvesting treatments with variable retention: (i) dispersed retention (DR) of 30 m^2 ha^{-1} (20–30% retention); (ii) aggregated retention (AR) with one aggregate per hectare and clear-cuts (28% retention); and (iii) combined dispersed and aggregated retention (DAR) with one aggregate per hectare and dispersed retention of 10–15 m^2 ha^{-1} (40–50% retention). Data analyses included parametric and permutational ANOVAs, multivariate classification and ordinations.

Before harvesting, 31 plant species were found, where richness, cover and biomass were directly related to site quality. The presence of canopy gaps did not have a significant impact on the measured variables. After harvesting, 20 new species appeared from adjacent associated environments (two from *N. antarctica* forests and 18 from grasslands and peatlands). At the stand level, understory values were higher in AR > DR > DAR > OGF. Most (81–95%) plant richness at baseline conditions was conserved in all treatments, where inside the aggregates understory remained similar to OGF. Combination of aggregated and dispersed retention (DAR) better limited exotic species introduction and protected sensitive species, improving conservation in harvested stands. Changes in understory variables were observed after the first YAH in all treatments; greater changes were observed in the harvested areas than in aggregates. Changes stabilized at the fourth YAH. As a conclusion, the location of retention aggregates should be selected to preserve species understory diversity of more speciose and diverse habitats or particularly uncommon stands. Implementation of different kinds (patterns and levels) of retention for improvement of biodiversity conservation in harvested forests should be included in timber and forest management planning.

1. Introduction

Understory plants provide a crucial role in maintaining the structure and function of forest ecosystems. They contribute to forest biodiversity, generate the initial competitive interactions with regeneration phases of dominant canopy species, determine energy flow and nutrient cycling, and respond complexly to both natural and anthropogenic disturbances (Gilliam, 2007). The ecosystem integrity of temperate forests depends on understory plant species conservation, as well as the stability and survival of other organisms, such us micro- and meso-fauna (Clement, 2001). However, understory plant species have heterogeneous abundance and

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distribution patterns, which depends on the overstory species and structure (e.g., site quality of the stands or gap presence) (e.g., Warner and Harper, 1972; Veblen et al., 1977, 1979; Goldblum, 1997; Hutchinson et al., 1999; Damascos and Rapoport, 2002; Small and McCarthy, 2005; Fahey and Puettmann, 2008), as well as of micro-environmental and stand conditions (e.g., Huebner et al., 1995; Thomas et al., 1999; Palmer et al., 2000; Fraterrigo et al., 2009). Natural and anthropogenic disturbances in forest ecosystems affect these conditioning factors and modify understory diversity and distribution (Chen et al., 1993; Ohlson et al., 1997; Jenkins and Parker, 1999; Økland, 2000; Martínez Pastur et al., 2010). Therefore, herbaceous vegetation could act as a useful indicator of forest sustainability, ecosystem health and conservation status (Hermy et al., 1999; Lindenmayer et al., 2000; Dale et al., 2002).

Harvest intensity is important in determining the magnitude of impacts on forest biodiversity and natural ecological cycles (Kohm and Franklin, 1997). The impact of traditional silvicultural practices (e.g., clear-cuts and shelterwood cuts) on understory plant diversity has been analyzed world-wide (e.g., Duffy and Meier, 1992; Elliot et al., 1997; Jenkins and Parker, 1999; Nagaike et al., 1999; Quinby, 2000; Martínez Pastur et al., 2002). Recently, the variable retention approach to timber harvesting emerged as an alternative silvicultural management proposal to mitigate harmful effects of traditional practices on forest ecosystems, where the major objectives are: (1) create "life-boating" species and processes over the regeneration phase, (2) increase structural variation in managed stands, and (3) enhance connectivity at the landscape level (Franklin et al., 1997). Variable retention benefits for understory conservation have been reported in North American, northern Europe and Australian temperate forests (North et al., 1996; Hazell and Gustafsson, 1999; Vanha-Majamaa and Jalonen, 2001; Aubry et al., 2004; Nelson and Halpern, 2005). However, there is a lack of information about the effectiveness of variable retention practices to improve understory vascular plant diversity conservation in southern Patagonian forests (Lencinas et al., 2008a). Also, few studies include medium- and long-term research to assess variable retention effects (Arnott and Beese, 1997; Hickey et al., 2001; Spence et al., 2002; Aubry et al., 2004; Martínez Pastur et al., 2010) or compare diversity structure before and after harvesting (Before–After-Control–Impact or BACI approach) as a way to determine the extent of variation in biodiversity prior to the implementation of silvicultural treatments (Vanha-Majamaa and Jalonen, 2001; Nelson and Halpern, 2005; Smith et al., 2008). Consequently, the objectives of this work were: (i) to define a baseline of understory plant diversity (cover, biomass and richness) in old-growth southern Patagonian *Nothofagus pumilio* forests (Argentina) comparing the influence of site quality and canopy gaps; (ii) to evaluate understory plant diversity conservation in variable retention harvested stands, compared to old-growth forests; and (iii) to assess temporal changes over a four-year time period after harvesting in harvested and old-growth stands. We expect that: (i) greater diversity occurs at higher site qualities and within canopy gaps; (ii) the inclusion of retention in harvested stands, as well as the combination of different retention types, improve the conservation of understory plant diversity; and (iii) the stability of understory plant diversity over time is related to the degree of retention used in the stands.

2. Materials and methods

2.1. Understory of southern Patagonian Nothofagus pumilio forests

At the austral extreme of South America, Tierra del Fuego Island, shared between Chile and Argentina, hosts the world's

southernmost forested ecosystems, which are also found in one of the least disturbed eco-regions on the planet (Mittermeier et al., 2003). *N. pumilio* is the main tree component of these forests in the central portion of the island. This species has a wide natural distribution from 36°50′ to 55°02′ S (Dimitri, 1972). Among the three types of *Nothofagus* found in southern Patagonia, *N. pumilio* forests are mainly used for timber harvesting activities due to good yield characteristics (Martínez Pastur et al., 2000). The understory of these timber quality stands in southern Patagonian *N. pumilio* forests comprises low vascular plant diversity (Lencinas et al., 2008b), including species from genus *Adenocaulon*, *Blechnum*, *Dysopsis*, *Galium*, *Osmorhiza*, *Ranunculus* and *Viola* under closed canopies, and *Acaena*, *Cardamine*, *Cotula*, *Gunnera*, *Rubus*, *Schizeilema* and *Senecio* under open canopies or more humid sites (Moore, 1983). A number of exotic plant species are also present, deliberately or accidentally introduced mainly from European meadows, e.g., *Cerastium fontanum*, *Poa pratensis*, *Rumex acetosella*, *Taraxacum officinale* and *Veronica serpyllifolia* (Moore and Goodall, 1977; Collantes and Anchorena, 1993).

2.2. Studied sites and forest structure characterization

A pure old-growth *Nothofagus pumilio* forest was selected in San Justo Ranch, Tierra del Fuego, Argentina (54°06′ S, 68°37′ W) with a full range of site qualities; the site index at base age of 60 years (SI_{60}) varied between less than 9.8–23.2 m. Stands growing on high-quality sites ($SI_{60} \geqslant 16.5$ m) have total volume over $650\ m^3\ ha^{-1}$ and trees with a total height over 24 m. On medium-quality sites ($SI_{60} = 13.1$–16.5 m), stands have a total volume of $700\ m^3\ ha^{-1}$ and trees with a total height between 20.5 and 24 m, while stands growing on low-quality sites ($SI_{60} \leqslant 13.1$ m) have a total volume of less than $550\ ha^{-1}$ and trees with a total height less than 20.5 m (Martínez Pastur et al., 1997). Canopy gaps are common in all site qualities and occur naturally by wind-throw (Rebertus and Veblen, 1993). These forests were undisturbed by forestry practices before silvicultural regeneration systems were in place.

Climate was measured in the study area with two weather stations (Davis Weather Wizard III and accessories, USA) placed in old-growth and harvested stands from 2002 to 2005 (Martínez Pastur et al., 2007). Weather conditions were characterized by short, cool summers and long, snowy and frozen winters. Mean monthly temperatures (2 m above the forest floor) varied from −0.2 to 10.4 °C (extreme minimum and maximum from −9.6 °C in July to 24.9 °C in February) in the old-growth forest, while in the harvested stand temperature varied from −1.0 to 10.6 °C (extremes from −11.3 °C in July to 25.9 °C in February). Only 3 months per year did not have mean monthly temperatures under 0 °C, and the growing season was approximately 5 months (Barrera et al., 2000). Soil temperatures at 30 cm deep were never below freezing in the old-growth forest, but soil freezing was observed in the harvested stand (−0.2 to −0.6 °C during June–July). Through fall precipitation including snowfall (2 m above the forest floor) was $382\ mm\ yr^{-1}$ inside the old-growth forest, while it was $639\ mm\ yr^{-1}$ in the harvested stand. Annual average wind speed outside forests was $8\ km\ h^{-1}$, reaching up to $100\ km\ h^{-1}$ during storms.

The study was conducted in a large permanent plot (61 ha) were the four treatments were applied. Each treatment included several stands, and retention treatments included at least six aggregates. Sampling was conducted in all stands of each treatment using a random polar coordinate design around a reference point in the center of each site (Tremblay and Larocque, 2001), 1 year before and 4 years after harvesting. Harvesting systems with a variable retention approach were applied during 2001 in stands of similar site quality, leaving 8.6 ha of old-growth forests as

controls (OGF) (22.9 m total height, 528 trees ha^{-1}, 40.6 cm diameter at breast height-DBH, 65.0 m^2 ha^{-1} basal area-BA and 727.8 m^3 ha^{-1} total over bark volume-TOBV). Studied harvesting systems were defined as: (i) 23.6 ha of dispersed retention (DR), where 30 m^2 ha^{-1} BA of the remnant overstory trees were regularly distributed throughout the area, representing 20–30% of green tree retention (105 trees ha^{-1}, 54.8 cm DBH and 353.7 m^3 ha^{-1} TOBV), which was comparable with the first cut of a traditional shelterwood cut management system (Schmidt and Urzúa, 1982; Martínez Pastur et al., 2000); (ii) 18.5 ha of aggregated retention (AR) with one aggregate per hectare (30 m radius) of primary forest and clear-cuts among them, representing 28% of retention; and (iii) 10.7 ha of combined dispersed and aggregated retention (DAR) with one aggregate per hectare (30 m radius) and dispersed retention (10–15 m^2 ha^{-1} BA) among them, representing 40–50% of retention. The general structure of these stands can be seen in Fig. 1.

2.3. Understory sampling

The understory vegetation was measured in each treatment during the summer season of five consecutive years, before and after harvesting. The baseline was defined 1 year prior to harvesting, and changes were measured in the next 4 years after harvesting (YAH), resulting in a repeated measures design. Before harvesting, sampling was done in high (SI$_{60}$ ⩾ 16.5 m) (HSQ), medium (SI$_{60}$ = 13.1–16.5 m) (MSQ) and low (SI$_{60}$ ⩽ 13.1 m) (LSQ) site quality stands. Likewise, we surveyed outside and inside canopy gaps (natural tree-fall with an average diameter of 23 m) in HSQ stands, which could be considered "big gaps," following Damascos and Rapoport (2002) canopy gap classification system. After harvesting, samples were taken in the same stands under the different previously described treatments (AR, DR and DAR), as well as control stands (OGF). Before and after harvesting, understory communities were studied with ten plots (1 m^2 each) in each treatment located through a random polar coordinate system, with an angle and a distance randomly selected and proportional to the stand area. The plot size was selected because biomass harvesting of woody species (less than 0.5 m tall), herbaceous vascular and non-vascular plants would have been more labor intensive if larger plots were used and this plot size also corresponded to previous work by Tremblay and Larocque (2001) and Martínez Pastur et al. (2002). For the baseline study a total of $N = 40$ plots (three site qualities × 10 plots, plus two locations inside and outside × five gaps) were used; for the comparison among regeneration treatments after harvesting a total of $N = 160$ plots (four treatments × 10 plots × 4 years) was measured. In treatments with aggregates (AR, DAR), sampling effort was proportional to the aggregated retention area with 30% of the plots distributed inside aggregates (in aggregated retention-ARI and combined retention-DARI) and 70% among them in harvested sectors (in aggregated retention-ARO and combined retention-DARO). Each plot was sampled only once and was subdivided in four 0.25 m^2 subplots orthogonally placed 5 m apart from a center (Martínez
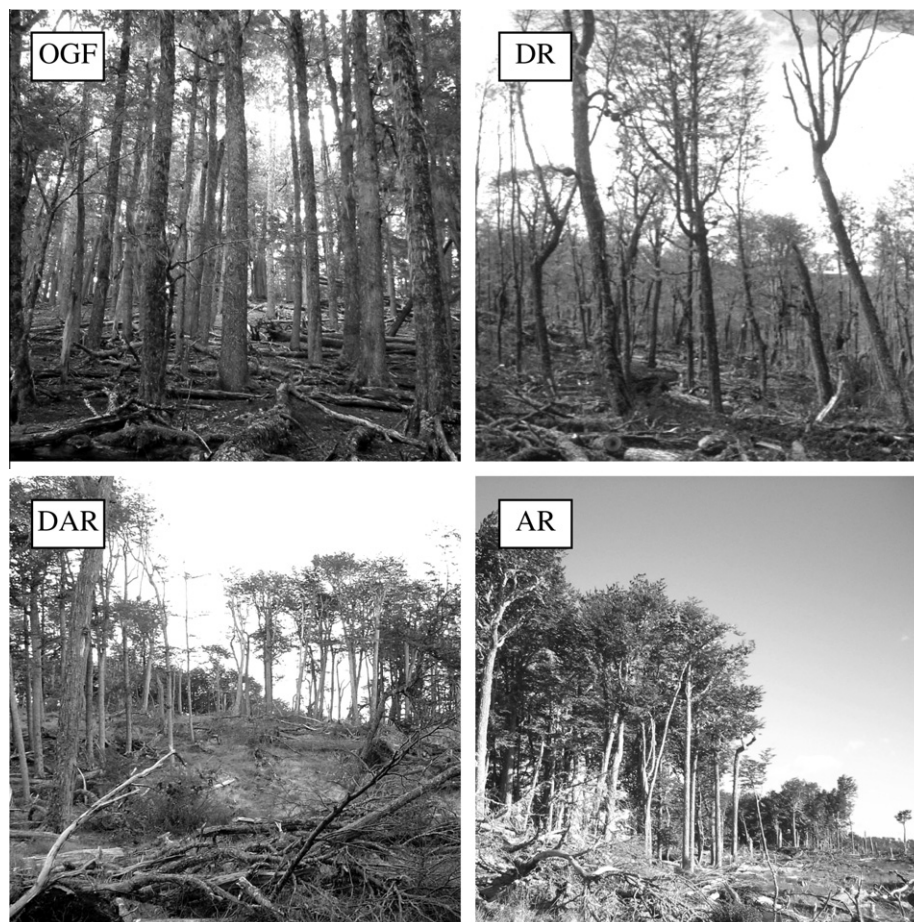

Fig. 1. Southern Patagonian *Nothofagus pumilio* silvicultural treatments: OGF = old-growth forests; DR = dispersed retention (note the regularity in the remnant tree distribution); DAR = combined retention (three aggregates are showed, with dispersed retention among them); AR = aggregated retention (three aggregates are showed, with clear-cut among them).

Pastur et al., 2002), while in each canopy gap eight 0.25 m² subplots were distributed in two positions (near and far to the gap centre) at each cardinal orientation point (north, west, east and south). Subdivision and separation of subplots leads to a better representativeness of understory forest communities (Martínez Pastur et al., 2002), but subplots were considered as one for the following analyzes.

In each subplot, vascular plants (Dicotyledonae, Monocotyledonae and Pteridophyta) were taxonomically classified by species, following Moore (1983) and Correa (1969–1988) and non-vascular plants (mosses and liverworts) were considered together in the same group (lower plants). Native and exotic classification of the observed plant species was done according to the proposal of Moore (1983). The percentage of forest floor cover (woody debris, bare forest floor or litter without vegetation, and total vegetation) was estimated by interception method in each subplot, using a square grid with 25 points per 0.25 m^{-2} (Mueller-Dombois and Ellenberg, 1974), and cover per plot was calculated by adding the four related subplots. All live aboveground plant material was collected at each subplot and dried in an oven at 70 °C until obtaining constant weight, which is the most accurate technique for biomass estimation (Catchpole and Wheeler, 1992).

2.4. Data analysis

Treatments were characterized and compared through alpha and beta diversity (Moreno, 2001). Alpha diversity was considered as the species richness measurement of a homogeneous community and was evaluated by number of species; beta diversity was the amount of change, or turnover, in species composition among communities within a landscape and was evaluated by the Whittaker (1960) index $\beta = s/(\alpha - 1)$, where s is the total number of species recorded in a system (e.g., two treatments), and α is the average species richness found within these communities (Whittaker, 1972). Species richness was selected as an appropriate indicator to characterize *Nothofagus* forests (Lencinas et al., 2008b), while the Whittaker beta index has demonstrated itself to be one of the most suitable for ecological analysis of community data (Wilson and Shimida, 1984). Beta diversity was only calculated for the fourth YAH data, as the maximum dissimilarity year.

For the baseline characterization, one-way ANOVAs were conducted with site quality and canopy gap presence as main factors. For comparison among regeneration treatments after harvesting, repeated measure ANOVAs were used. When the sphericity test was significant, Greenhouse and Geisser (1959) univariate adjustment was applied to evaluate within-subjects effects. Averages were tested for significant differences by Tukey test ($p < 0.05$). The response variables in all the analyzes were: (i) cover (%) and biomass (kg ha^{-1}) of *N. pumilio* juveniles (less than 0.5 m tall) and lower plants; (ii) cover, biomass and average richness (species per plot) of other dicots, monocots, Pteridophyta, and total vegetation; and (iii) cover of woody debris and bare forest floor. For average richness, plants were also grouped into native and exotic species. Statistica (Statsoft, USA) and Statgraphics (Statistical Graphics Corp., USA) software were used for these analyzes.

Permutational multivariate ANOVA (PERMANOVA, Anderson, 2005) and a permutational test of multivariate dispersion (PERMDISP, Anderson, 2004) were conducted to test effects of unharvested (OGF, DARI and ARI) vs. harvested (DARO, ARO and DR) treatments. Also, non-metric multidimensional scaling ordination analysis (NMS) was carried out with presence–absence data for the first four YAH, using Bray–Curtis distance, to support the visual assessment of these patterns (Anderson, 2005). PERMANOVA, PERMDISP and NMS analyses were conducted on the same matrix, using Bray–Curtis distances and 9999 unrestricted random permutations of the raw data. Then, different retention types and

old-growth forests were clustered using Ward's method of linkage with Euclidean distance measurement (Digby and Kempton, 1987) based on a matrix of accumulated plant species composition during the first four YAH. Finally, a detrended correspondence analysis (DCA) was conducted to evaluate the changing magnitude in plant species composition between the first and the fourth YAH, using a presence–absence data matrix, without down weight for rare species and with axis rescaling (Manly, 1994). DCA was selected because this is the only ordination technique that simultaneously analyzes sampling units and species, allowing the examination of ecological interrelationships between them in a single-step analysis (Ludwig and Reynolds, 1988). In all multivariate analyses, treatments were OGF, DR, ARI, ARO, DARI and DARO. PC-Ord (McCune and Mefford, 1999) and Statistica (Statsoft, USA) software were used for these analyzes.

3. Results

A total of 51 vascular plant species were classified along the study of which 10 were exotics (Appendix Tables A–C). Prior to harvesting, 31 species were found (six exotics) in the old-growth forests, where species richness was directly related to the site quality of the stands (11 species for LSQ, 22 species for MSQ and 24 species for HSQ) or canopy opening (29 species for gaps). These species were classified as follows (Appendix Tables A–C): (i) characteristic of primary *N. pumilio* forests: 21 species (three exotics), because they were well represented in both MSQ and HSQ stands; (ii) introduced from *N. antarctica* forests: four species; and (iii) introduced from grassland and peat-lands: six species (three exotics), the last two groups being more frequently observed in gaps.

In the baseline characterization, significant differences were found among sites of different quality for cover of dicots, lower plants, total vegetation, woody debris and bare forest floor; for biomass of *N. pumilio* juveniles, dicots and lower plants; and for average richness of dicots, monocots, total vegetation and native species (Table 1). HQS had the greatest values for cover and biomass of dicots (41.5% and 231 kg ha^{-1}, respectively) and biomass of *N. pumilio* juveniles (111 kg ha^{-1}) compared to the other quality site stands. Meanwhile differences were not found between HSQ and MSQ stands for total vegetation cover (50.9%) and richness of dicots (7.4), monocots (2.0), total vegetation (9.8) or native species (9.0). Beside this, MSQ had the highest richness of exotic species (1.2), and LQS showed the greatest cover and biomass of lower plants (13.5% and 844 kg ha^{-1}, respectively), as well as cover of woody debris (22.4%) and bare forest floor (58.0%). No significant differences were detected for most of the variables when canopy openings were analyzed (Table 2), except for bare forest floor cover, which was greater in closed canopy than in gaps ($F = 5.16$, $p = 0.036$).

After harvesting, 20 new species appeared in the harvested stands, compared with the baseline; two species came from *N. antarctica* forests and 18 species (four exotics) from grasslands and peatlands (Appendix Tables A–C). OGF had the lowest total species richness (33 species) along the whole study, and AR was the most speciose treatment (45 species), while DAR and DR had intermediate values (35 and 41 species, respectively). At the fourth YAH, beta diversity varied from 1.17 to 1.38, with OGF being more similar to DAR (1.32) than to AR (1.34) or DR (1.35). Comparison among harvested treatments showed DAR was equally similar to DR and AR (1.17), followed by DR–AR (1.18).

The greatest species introduction compared to the baseline was observed in ARO (24 species in the whole study period), and this was steeply increasing from the first YAH (11 species) to the fourth YAH (22 species) (Fig. 2). In DR, 23 introduced species were observed in the whole study period (2–21 species from 1 to 4 YAH, respectively). Alternatively, a low rate of introduction (17

Table 1
One-way ANOVA for cover, biomass and average richness of understory plants in three site qualities (HSQ with $SI_{60} > 16.5$ m, MSQ with SI_{60} between 13.1 and 16.5 m, LSQ with $SI_{60} < 13.1$ m) at the baseline before harvesting in old-growth *Nothofagus pumilio* forests.

Variable	HSQ	MSQ	LSQ	F (p)
Understory cover (%)				
N. pumilio juveniles	5.59	5.34	3.16	1.84 (0.178)
Other dicots	41.54 c	27.74 b	2.52 a	34.31 (<0.001)
Monocots	3.97	6.48	0.42	2.26 (0.123)
Pteridophyta	0.15	0.15	0.00	1.07 (0.356)
Lower plants	6.13 a	4.83 a	13.50 b	7.12 (0.003)
Total vegetation	57.38 b	44.54 b	19.6 a	17.97 (<0.001)
Woody debris	11.82 a	16.29 ab	22.35 b	3.98 (0.030)
Bare floor	29.90 a	38.57 a	57.95 b	9.56 (<0.001)
Understory biomass (kg ha⁻¹)				
N. pumilio juveniles	111.6 b	68.4 ab	36.1 a	3.53 (0.043)
Other dicots	230.9 c	99.5 b	6.9 a	23.41 (<0.001)
Monocots	32.1	21.8	2.4	2.19 (0.131)
Pteridophyta	0.4	0.3	0.0	0.88 (0.426)
Lower plants	424.7 ab	288.6 a	844.3 b	3.54 (0.043)
Total vegetation	799.8	478.6	889.6	1.94 (0.164)
Understory richness (species per plot)				
Dicots	7.4 b	7.5 b	3.5 a	32.37 (<0.001)
Monocots	1.9 b	2.1 b	0.4 a	11.54 (<0.001)
Pteridophyta	0.04	0.03	0.01	0.88 (0.426)
Total vegetation	9.5 b	10.0 b	3.9 a	33.88 (<0.001)
Natives	9.1 b	8.8 b	3.8 a	29.88 (<0.001)
Exotics	0.4 a	1.2 b	0.1 a	9.81 (<0.001)

F (p) = *F* test with significance level between parentheses. Values followed by different letters in each row are significantly different with Tukey test at *p* < 0.05.

Table 2
One-way ANOVA for cover, biomass and average richness of understory plants in closed canopy and gaps in high quality sites ($SI_{60} > 16.5$ m) at the baseline before harvesting in old-growth *Nothofagus pumilio* forests.

Variable	Closed	Gaps	F (p)
Understory cover (%)			
N. pumilio juveniles	5.59	4.62	0.36 (0.558)
Other dicots	41.54	40.70	0.01 (0.906)
Monocots	3.97	9.27	1.79 (0.198)
Pteridophyta	0.15	1.33	1.60 (0.221)
Lower plants	6.13	10.13	2.55 (0.128)
Total vegetation	57.38	66.06	1.03 (0.323)
Woody debris	11.82	15.40	0.60 (0.447)
Bare floor	29.90 b	18.54 a	5.16 (0.036)
Understory biomass (kg ha⁻¹)			
N. pumilio juveniles	111.6	110.4	0.00 (0.978)
Other dicots	230.9	297.8	1.07 (0.316)
Monocots	32.1	81.8	2.33 (0.144)
Pteridophyta	0.4	31.0	2.74 (0.116)
Lower plants	424.7	702.1	1.77 (0.200)
Total vegetation	799.8	1223.1	3.86 (0.065)
Understory richness (species per plot)			
Dicots	7.4	6.6	0.84 (0.372)
Monocots	1.9	2.9	2.83 (0.110)
Pteridophyta	0.2	0.6	1.80 (0.196)
Total vegetation	9.5	10.1	0.14 (0.713)
Natives	9.1	9.6	0.11 (0.747)
Exotics	0.4	0.5	0.13 (0.722)

F (p) = *F* test with significance level between parentheses. Values followed by different letters in each row are significantly different with Tukey test at *p* < 0.05.

species) was found in DARO (6–15 species from 1 to 4 YAH). ARI and DARI showed the lowest values of introductions (2 and 3 species in the whole study period, respectively) with few variations among YAH (only two species from 1 to 4 YAH for ARI, and 1–3 species for DARI), meanwhile OGF had 12 species introductions, which varied from 4 to 7 from 1 to 4 YAH).

Over the entire study period, a loss of characteristic *N. pumilio* forest plant species was observed in harvested treatments, and this was the same in DR, DARO and DARI (three species). Meanwhile only one species was lost in ARO and none in ARI. However, annual variations in loss of characteristic species were observed: 6–3 in

DARI and DARO > 5–3 in DR > 5–2 in ARI > 4–2 in ARO > 4–1 in OGF. Compared to baseline richness, a high proportion of characteristic species of primary *N. pumilio* forests were conserved in all treatments (between 71% and 95%) (Fig. 2).

In the post-harvesting samplings, repeated measures ANOVA showed significant differences among treatments for all covers (Table 3). Juveniles of *N. pumilio*, monocots and lower plant covers were greater in DR than in other treatments (4.6% and 4.5%, respectively), meanwhile other dicot cover was highest in DAR (32.5%) and AR (27.3%). Harvested stands did not differ in woody debris, bare forest floor and total vegetation cover, but they did with OGF: woody debris
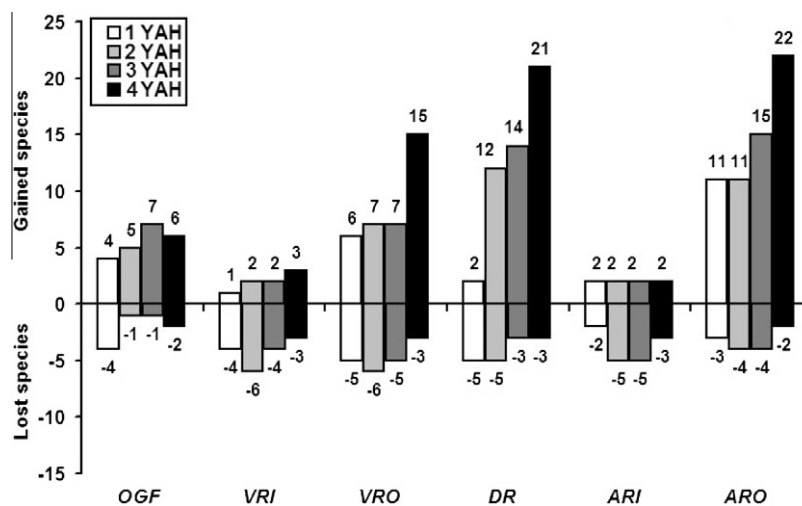
Fig. 2. Gained and lost understory plant species during the first 4 years after harvesting (YAH) at different treatments (OGF = old-growth forests; DARI = combined retention inside aggregates; DARO = combined retention outside aggregates; DR = dispersed retention; ARI = aggregated retention inside aggregates; ARO = aggregated retention outside aggregates) compared with the species richness detected during the baseline in *Nothofagus pumilio* forests.

Table 3
Repeated measures ANOVA for understory cover (%) during the first 4 years after harvesting (YAH) in old-growth and harvested stands in *Nothofagus pumilio* forests.

Source	df	*N. pumilio* juveniles	Other dicots	Monocots	Pteridophyta	Lower plants	Woody debris	Bare floor	Understory total vegetation
Between subject effects									
A: treatments	3	4.23 (0.012)	12.28 (<0.001)	5.30 (0.004)	2.60 (0.067)	5.03 (0.005)	6.36 (0.001)	33.01 (<0.001)	9.23 (<0.001)
Within subject effects									
B: YAH	3	2.13 (0.127)	2.99 (0.034)	1.65 (0.195)	1.19 (0.302)	1.22 (0.304)	1.70 (0.170)	6.04 (<0.001)	4.26 (0.007)
Interaction									
A × B	9	1.23 (0.300)	0.82 (0.600)	1.07 (0.389)	1.24 (0.303)	0.97 (0.455)	1.01 (0.437)	0.54 (0.839)	0.89 (0.532)
Treatments	OGF	2.32 a	11.41 a	3.72 a	0.01	2.29 a	23.27 a	56.97 b	19.76 a
	DAR	2.18 a	32.47 c	2.94 a	0.03	2.50 a	34.18 b	25.69 a	40.13 b
	DR	4.60 b	18.04 ab	8.49 b	0.00	4.50 b	35.15 b	29.23 a	35.62 b
	AR	2.44 a	27.29 bc	6.33 ab	0.20	2.12 a	37.19 b	24.42 a	38.38 b
YAH	1	2.94	17.32 a	3.45	0.05	3.50	30.22	42.51 b	27.26 a
	2	2.66	24.46 ab	6.19	0.05	2.40	29.76	34.48 ab	35.76 a
	3	2.06	21.45 ab	5.22	0.00	3.09	36.22	32.96 a	31.81 a
	4	3.89	25.99 b	6.63	0.14	2.42	33.58	27.35 a	39.07 b

OGF = old-growth forest; DR = dispersed retention; DAR = combined (dispersed and aggregated) retention; AR = aggregated retention; $F(p)$ = F test with significance level between parentheses. Values followed by different letters in each column are significantly different with Tukey test at $p < 0.05$.

and total vegetation covers were lower in OGF (23.3% and 19.8%, respectively) than in harvested stands (34.2–37.2% and 35.6–40.1%, respectively), while bare forest floor cover was higher in OGF (57.0%) than in harvested stands (24.4–25.7%). YAH effects were significantly different for only three variables, being maximum at the fourth YAH for total vegetation and dicots cover (26.0% and 39.1%, respectively), and at the first YAH for bare forest floor cover (42.5%). Interactions were not significant for all cover variables ($F < 1.24$, $p > 0.300$).

In biomass analyses, repeated measures ANOVA showed significant differences among treatments and YAH for all variables except Pteridophyta (Table 4), with the greatest values for *N. pumilio* juveniles and lower plant biomass in DR (117 and 426 kg ha^{-1}, respectively), for other dicot biomass in AR (737 kg ha^{-1}), and for monocot biomass in DR (242 kg ha^{-1}) and AR (240 kg ha^{-1}). Total understory vegetation biomass was significantly lower in OGF (201 kg ha^{-1}) than in harvested stands (1000–1251 kg ha^{-1}), without significant differences among them. All significant biomass variables increased when YAH increased, except for lower plants which decreased with time. As in cover, interactions were not significant for biomass variables ($F < 1.48$, $p > 0.184$).

Understory richness variables showed significant differences among treatments in repeated measure ANOVAs (Table 5) except

for monocots and native species, but not for YAH except in exotic species. AR showed more dicots (6.0), Pteridophyta (0.2), total (8.3) and exotic (1.2) richness than other treatments, with values being smaller for OGF (4.9, 0.0, 6.2 and 0.5, respectively). In the fourth YAH, exotic richness outnumbered the previous values (1.3 vs. 0.5–0.7, respectively). Interactions were not significant either in average richness variables ($F < 2.00$, $p > 0.063$), except for native species ($F = 2.34$, $p = 0.019$). Interaction can be explained due to native average richness showed maximum, minimum and intermediate values for different years among treatments, e.g., second YAH had minimum native average richness in AR, maximum in DAR, and intermediate values in DR and OGF. Meanwhile, third YAH had minimum native average richness in DAR, maximum in DR, and intermediate values in AR and OGF.

NMS ordination of plant species composition showed great similarity among sample locations of old-growth stands and treatments (OGF, DARI and ARI), and dissimilarity among harvested treatments (DARO, ARO and DR) (Fig. 3). Particularly, significant differences were detected by PERMANOVA for centroid position of both groups ($F = 9.98$, $p \leqslant 0.01$) and by PERMDISP for dispersion ($F = 7.98$, $p = 0.01$). Cluster analysis (Fig. 4) had comparable results to those described for NMS, where classification of treatments showed a close relation between DARI and ARI (2.45 Euclidean dis-

Table 4
Repeated measures ANOVA for understory plant biomass (kg ha^{-1}) during the first 4 years after harvesting (YAH) in old-growth and harvested stands in *Nothofagus pumilio* forests.

Source	df	*N. pumilio* juveniles	Other dicots	Monocots	Pteridophyta	Lower plants	Understory total vegetation
Between subject effects							
A: treatments	3	5.41 (0.004)	10.29 (<0.001)	6.59 (0.001)	1.94 (0.141)	6.79 (<0.001)	12.71 (<0.001)
Within subject effects							
B: YAH	3	3.49 (0.034)	7.29 (<0.001)	3.48 (0.037)	0.81 (0.423)	4.04 (0.024)	4.18 (0.008)
Interaction							
A × B	9	1.24 (0.292)	1.48 (0.184)	1.29 (0.274)	0.83 (0.527)	0.81 (0.557)	0.90 (0.527)
Treatments	OGF	28.7 a	44.5 a	18.6 a	0.1	158.7 a	200.5 a
	DAR	56.0 ab	613.9 bc	92.1 ab	0.1	237.9 a	1000.0 b
	DR	116.8 b	261.4 ab	241.6 b	0.0	425.6 b	1045.4 b
	AR	63.6 a	736.9 c	240.4 b	3.9	206.4 a	1251.3 b
YAH	1	54.0 ab	200.7 a	52.2 a	2.1	412.1 b	721.1 a
	2	47.1 a	531.9 bc	146.7 ab	0.2	215.7 a	941.7 ab
	3	55.0 ab	304.1 ab	150.4 ab	0.0	207.6 a	717.1 a
	4	109.0 b	620.0 c	243.4 b	1.7	193.3 a	1167.3 b

OGF = old-growth forest; DR = dispersed retention; DAR = combined (dispersed and aggregated) retention; AR = aggregated retention; *F* (*p*) = *F* test with significance level between parentheses. Values followed by different letters in each column are significantly different with Tukey test at *p* < 0.05.

Table 5
Repeated measures ANOVA for understory richness (species per plot) during the first 4 years after harvesting (YAH) in old-growth and harvested stands in *Nothofagus pumilio* forests.

Source	df	Dicots	Monocots	Pteridophyta	Total	Natives	Exotics
Between subject effects							
A: treatments	3	4.31 (0.011)	2.78 (0.055)	3.84 (0.017)	3.49 (0.025)	2.09 (0.119)	2.85 (0.051)
Within subject effects							
B: YAH	3	1.69 (0.174)	1.71 (0.168)	1.94 (0.158)	2.35 (0.092)	0.61 (0.607)	6.96 (<0.001)
Interaction							
A × B	9	1.66 (0.108)	1.52 (0.150)	1.53 (0.193)	2.00 (0.063)	2.34 (0.019)	1.81 (0.074)
Treatments	OGF	4.85 a	1.38	0.02 a	6.15 a	5.80	0.45 a
	DAR	5.52 ab	1.40	0.05 ab	6.98 ab	6.22	0.75 ab
	DR	5.08 ab	2.05	0.01 a	7.12 ab	6.42	0.70 ab
	AR	5.95 b	2.10	0.20 b	8.25 b	7.10	1.15 b
YAH	1	5.22	1.55	0.05	6.82	6.38	0.45 a
	2	5.05	1.60	0.08	6.72	6.10	0.62 a
	3	5.50	1.65	0.01	7.15	6.45	0.70 a
	4	5.62	2.12	0.15	7.90	6.62	1.28 b

OGF = old-growth forest; DR = dispersed retention; DAR = combined (dispersed and aggregated) retention; AR = aggregated retention; *F* (*p*) = *F* test with significance level between parentheses. Values followed by different letters in each column are significantly different with Tukey test at *p* < 0.05.

tances), and these were secondarily related to OGF (3.95 Euclidean distances). Finally, the last group included DARO and DR (3.15 Euclidean distances) that joined with ARO to a greater distance (4.10 Euclidean distances).

In DCA, the center of the first and the fourth YAH sampling for each treatment was represented to highlight the magnitude change in species diversity (Fig. 5). DARI and ARI showed smaller changes, while DR had the greatest one. Axis 1 was mainly related to YAH, while Axis 2 could be related to the soil moisture gradient or ecological preferences of the species. Characteristic species of old-growth forests were observed in the central zone of the DCA species graphic, and close to the right, the introduced ones from *N. antarctica* forests. Introduced species coming from grasslands and peatlands were placed in the periphery of the graphic.

4. Discussion

4.1. Baseline before harvesting

Total baseline understory plant species richness in southern Patagonian *N. pumilio* OGF (21 species) was found to be lower than Northern Hemisphere primary temperate forests (e.g., from 45 to 69 species, Warner and Harper, 1972; Boncina, 2000; Quinby,

2000; Nelson and Halpern, 2005), but it was comparable to other Patagonian *N. pumilio* forests (19 species for Martínez Pastur et al., 2002; 26 species for Damascos and Rapoport, 2002) and old-growth forests at similar latitudes even in the north (e.g., 13–16 species in eastern Canadian forests, Tremblay and Larocque, 2001). However, understory biomass was rather low in OGF (478–889 kg ha^{-1}) compared with other temperate forests (e.g., 420–1170 kg ha^{-1}, Warner and Harper, 1972; and 660–3930 kg ha^{-1}, Tremblay and Larocque, 2001). Low understory plant diversity in Tierra del Fuego forests is thought to occur due to extreme climatic conditions during the growing season: short growth period (Roig et al., 2002), low average temperatures, and low thermal amplitude between winter and summer (Ferreyra et al., 1998).

In this study, understory plant diversity (mainly dicots) was positively correlated with site quality in OGF, except for lower plants. Positive and negative association of vascular plant species with site quality also has been observed in other forests (Warner and Harper, 1972; Hutchinson et al., 1999; Small and McCarthy, 2005), as well as between biomass productions with site quality (Warner and Harper, 1972). In Tierra del Fuego, site quality of the stands is mainly determined by abiotic factors (e.g., soil nutrient contents, soil drainage and depth, slope, aspect, topography and wind exposure) (Martínez Pastur et al., 1997), which influence both overstory structure and understory diversity (Martínez Pastur
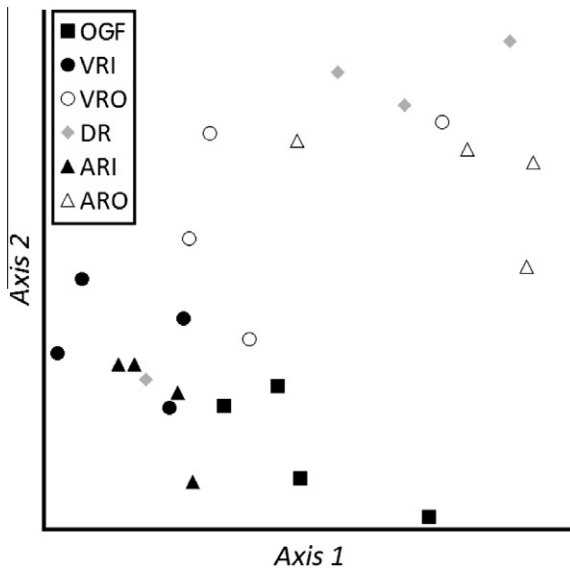
Fig. 3. Non-metric multidimensional scaling ordination analysis (final stress = 23.80, final instability = 0.054) with presence–absence understory plant species data during the first 4 years after harvesting at different treatments in *Nothofagus pumilio* forests (OGF = old-growth forests; DARI = combined retention inside aggregates; DARO = combined retention outside aggregates; DR = dispersed retention; ARI = aggregated retention inside aggregates; ARO = aggregated retention outside aggregates).

Fig. 4. Treatment classification with presence–absence understory plant species data during the first 4 years after harvesting in *Nothofagus pumilio* forests (OGF = old-growth forests; DARI = combined retention inside aggregates; ARI = aggregated retention inside aggregates; DARO = combined retention outside aggregates; DR = dispersed retention; ARO = aggregated retention outside aggregates).

et al., 2002). High soil moisture and light availability also increase southern Patagonian understory diversity (e.g., riparian forests) (Lencinas et al., 2008b; Veblen et al., 1977, 1979), as does habitat and microenvironment diversity (e.g., pits and mounds, rocks, woody debris in the forest floor) commonly observed in *Nothofagus* forests (Ramírez et al., 1985; Martínez Pastur et al., 2002). Understory plant species assembly could present a non-random nested subset pattern as a consequence of nested habitat distribution, which implies habitat rich patches will support nearly all species, and habitat poor patches only generalists (Honnay et al., 1999). This could explain the greater cover and biomass of lower plants in LSQ, where patches with high coarse woody debris cover are common. Here, moss establishment is facilitated by greater availability of suitable substrates, as well as by lower competition for
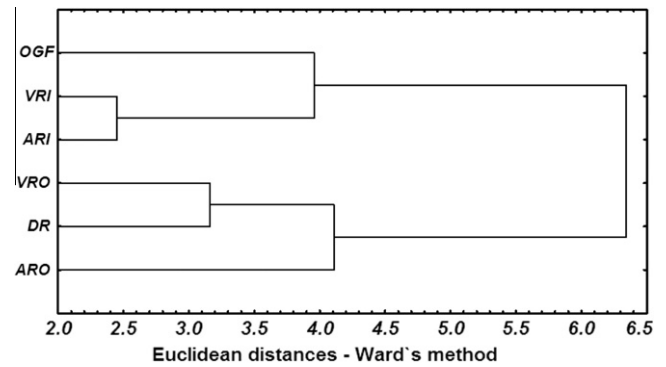
water and light at understory level with vascular plants compared to higher site quality stands. Finally, modifications in the overstory canopy (e.g., gaps) change microclimate and available resources at the understory level (e.g., soil moisture, light and temperature), compared to closed forests (Veblen et al., 1977, 1979; Veblen, 1985; Heinemann et al., 2000; Promis et al., 2010), and effects are mainly related to gap size, degree of disturbance and time since gap creation (Goldblum, 1997; Damascos and Rapoport, 2002; Fahey and Puettmann, 2008). In this study, gap presence did not greatly influence understory plant diversity, as was also observed for northern Patagonian *N. pumilio* forests by Damascos and Rapoport (2002), although there is significantly less bare forest floor or litter without vegetation in gaps. Lack of differences could be explained by gap micro-heterogeneity (Heinemann et al., 2000) and an unusually high proportion of generalist plants vs. shade-tolerant/intolerant species (Damascos and Rapoport, 2002). On the other hand, high values of richness and biomass in gaps could be masked by interactions among gap presence and site quality, because only gaps in better quality sites were analyzed, and the greatest values of understory diversity were observed in HSQ closed forests compared to MSQ or LSQ. However, total species richness inside southern Patagonian forest gaps increased 50%

Fig. 5. Detrended correspondence analysis to compare first to fourth year after harvesting (YAH) understory plant species diversity in *Nothofagus pumilio* forests (OGF = old-growth forests; DARI = combined retention inside aggregates; DARO = combined retention outside aggregates; DR = dispersed retention; ARI = aggregated retention inside aggregates; ARO = aggregated retention outside aggregates). Lines indicate magnitude of plant species change in the same treatment. Species codes figure in Appendix A.

compared to closed forests, which is similar to the understory of tree-fall gaps in other temperate forests (Goldblum, 1997).

4.2. Harvesting impacts on understory diversity

In *N. pumilio* forests, total understory vascular plant species richness (51 species), including old-growth and retention stands, is higher than in shelterwood cut harvested stands (35 species; Martínez Pastur et al., 2002). Shrub diversity is represented by only three species: *Berberis buxifolia*, *Chiliotrichum diffusum* and *Ribes magellanicum*, probably due to low resource availability and little ability of these species to compete with trees and herbs (Huston, 1994). Exotic plant richness, which competes with native vegetation for resources and niches (Moore and Goodall, 1977), is also higher in this work (10 species) than results reported previously in Martínez Pastur et al. (2002) (six species). Some of the observed exotic plants (*Cerastium fontanum*, *Poa pratensis*, *Rumex acetosella* and *Veronica serpyllifolia*) are naturalized and grow freely in both disturbed and undisturbed communities (Moore, 1983), due to abilities to disperse and acclimatize. Relative abundance of other exotic plants is associated with seed dispersal mechanisms such as anemochore species like *Taraxacum officinale* that increase their frequency in windy areas (Lencinas et al., 2008b). Finally, *Agoseris coronopifolium*, *Capsella bursa-pastoris*, *Phleum pratense*, *Senecio vulgaris* and *Stellaria media* were other exotics found here, but occurred mainly in disturbed soils (Moore, 1983; Roig, 1998).

In this study, different silvicultural regeneration systems stimulated the introduction of native and exotic species into harvested stands from associated environments (grasslands, peat-lands and *N. antarctica* forests), reducing beta diversity between habitats. The facilitation of these introductions is related to harvesting intensity (24 species in ARO, 23 in DR and 17 in DARO vs. three species in DARI and two in ARI) and time since disturbance (highest values were found at the fourth YAH). Species introductions into variable retention treatments were also observed in other retention-harvested forests: harvested stands gain nine understory early-seral species two YAH, while aggregates gain two forest species and 0–1 early-seral species (Nelson and Halpern, 2005). Similar to the effects on richness, understory cover and biomass of southern Patagonian harvested forests increased according to level of modifications of the overstory structure, following the sequence AR > DR > DAR. Rapid invasion of early successional species usually explained the greater understory cover in the clear-cut compared to that of green tree retention (Arnott and Beese, 1997). Moreover, the positive influence of light availability and precipitation produced two to three fold greater biomass in open compared to closed stands (Telfer, 1972). We know that harvesting intensity is usually proportional to the changes in microclimatic factors and resource availability at the understory level (e.g., radiation and effective rainfall) (Chen et al., 1993, 1995; Promis et al., 2010), which improves growth of many species at the understory level (Martínez Pastur et al., 2002; Honnay et al., 2002). The use of BACI approach in this study allowed us to avoid attributing understory changes to pre-harvesting differences, as was criticized by North et al. (1996).

Although pioneer species introduction in harvested stands can still be absent in the first post-treatment season (Vanha-Majamaa and Jalonen, 2001), changes in understory composition were observed beginning in the first YAH in these harvested stands, and increased with time. Incremental changes with time after harvesting could be due to increasing differences in soil texture and chemistry by less litter incorporation into the forest floor (Økland et al., 1999). Presence of newly exposed soil by litter removal generated by skidders or log movement during harvesting could also favor ruderal (defined as species that are first to colonize disturbed

lands) introduction, as was observed in tips and mounds that show a high proportion of annual/biennal plants (Palmer et al., 2000). Usually, new forests contain higher proportion of ruderal strategist plants than older forests, whereas old-growth forests are more characterized by stress tolerant strategists (Graae and Sunde, 2000). The shift from weedy invaders to residual species would be expected to occur with time (Roberts and Gilliam, 1995), depending on the origin of propagules, phenological traits and potential for vegetative expansion (Halpern, 1989).

Unexpectedly, adjacent old-growth forests had greater species richness after harvesting than the baseline (4–7 species from 1 to 4 YAH), although increments were stabilized at the fourth YAH. Random location of OGF plots in different aspects (east vs. west) before and after harvesting, as well as different distances to associated environments (*N. antarctica* patches in wetlands or edges), could result in higher presence of rare or less frequent species. Also, changes in understory richness of old-growth forests could be attributed to annual plant community fluctuations (Smith et al., 2008); due to changes in precipitation and temperature patterns among years and their effects as primary drivers of plant phenology (Nelson and Halpern, 2005). However, harvesting modifies microclimatic conditions not only inside harvested areas but also in the surrounding old-growth forests (e.g., in wind permeability), which facilitate dispersion of anemochore species like *Chiliotrichum diffusum*. Beside this, harvested stands increase food availability for some fauna, including the native ruminant *Lama guanicoe* (Martínez Pastur et al., 1999a) and for frugivorous and granivorous birds (Deferrari et al., 2001; Lencinas et al., 2009), which increases the use of these habitats and the OGF stands surrounding them too. The ultimate result, therefore, is to facilitate the introduction of plant species with animal dispersal mechanisms (e.g., *Bromus unioloides*).

On the other hand, variable retention harvesting of *N. pumilio* forest produced local extinctions (e.g., *Viola magellanica*) or a decrease in the relative abundance (e.g., *Adenocaulon chilensis*) of extremely sensitive understory species. In other temperate forests, species loss under variable retention (e.g., two species in two YAH period; Nelson and Halpern, 2005) are mainly related to soil disturbances under different retention patterns, being more frequent in pure aggregated treatments (with clear-cut among them) than in dispersed treatments (Aubry et al., 2004). The absence of a particular species in post-harvesting years may be attributed to harvesting impacts on microclimatic and site conditions, to natural variations in plant life history characteristics, or a combination of these factors (Smith et al., 2008). Species classified as locally extirpated may have been dormant or simply not detected in the post-harvest sampling years, and others that initially persist through the harvest disturbance may be gradually extirpated as a result of disturbance-related stress, inability to adapt to microclimate changes, and increased competition with ruderal species (Halpern et al., 2005). Sensitive species to disturbances also often have narrow requirements for habitat conditions (Gilliam, 2007) and frequently are present at naturally low densities in old-growth forests (e.g., <9%; Smith et al., 2008). Therefore, they have more probability to be affected by forest management practices, but in *N. pumilio* forests, sensitive species may actually present greater frequencies (<20%). In fact, one of these (*V. magellanica*) indeed had a relatively high natural abundance (33% frequency in OGF). The loss of this clonal species, which completely disappeared in DR and DAR, but not in AR, was probably associated with their patchy distribution generated by asexual propagation under closed canopies, as is observed for other forest clonal species (Kudoh et al., 1999). The overall loss of species from *N. pumilio* OGF (5–19% of baseline richness) during the first four YAH also suggests annual

fluctuations of understory species, as has been observed by Smith et al. (2008).

Aggregates of retention in both DAR and AR *N. pumilio* forests act as understory vegetation reserves, allowing for survival and/or better growth of species sensitive to canopy openings (e.g., *Uncinia lechleriana*), as was observed by Hazell and Gustafsson (1999) and Nelson and Halpern (2005) for some species (usually late-seral) and species groups. It is well represented by closeness between VRI and ARI plots with OGF in multivariate analyses. Patterns of retention seem to be more important than quantity for support populations that disappear from or decline substantially in harvested areas, because higher (70%) but dispersed retention levels present mechanical damage and edge effects at the entire stand that do not support late successional species, compared to lower

(50%) but aggregated retention (Vanha-Majamaa and Jalonen, 2001). On the other hand, the virtual absence of disturbed soil inside VRI and ARI may have limits on the establishment of introduced species (only 1–3 species in four YAH), as was also observed by Palmer et al. (2000) and Nelson and Halpern (2005).

In summary, species classified as late-seral show a strong affinity for old-growth and forest interior environments, characterized by patches of deep shade and cool, moist, and relatively stable ground-layer microclimates (Chen et al., 1993, 1995), as well as for stand structures that resemble old-growth forests (Spies, 1991; Peet and Christensen, 1988). For example, fungi and lichens need long tree-stand continuity (Økland, 2000) not *per se*, but associated with several factors, such as continuity of recently disturbed patches and continuous presence of a species-rich tree layer that

Appendix Table A

Classification of observed understory vascular plant species in old-growth and harvested *Nothofagus pumilio* forests, by taxonomic family and origin.

Specific names and authors	Family	Origin	Code
Old growth *Nothofagus pumilio* forest species			
Acaena magellanica (Lam.) Vahl 1804	Rosaceae	Native	ACMA
Acaena ovalifolia Ruiz and Pavón 1798	Rosaceae	Native	ACOV
Adenocaulon chilense Less. 1831	Asteraceae	Native	ADCH
Berberis buxifolia Lam. 1792	Berberidaceae	Native	BEBU
Blechnum penna-marina (Poiret) Khun 1868	Blechnaceae	Native	BLPE
Cardamine glacialis (Forster f.) DC 1821	Apiaceae	Native	CAGL
Cerastium fontanum Baumg. 1816	Caryophyllaceae	Exotic	CEFO
Cystopteris fragilis (L.) Bernh. 1806	Athyriaceae	Native	CYFR
Dysopsis glechomoides (A. Richard) Müller Arg. 1866	Euphorbiaceae	Native	DYGL
Festuca magellanica Lam. 1788	Poaceae	Native	FEMA
Galium antarcticum Hooker f. 1847	Rubiaceae	Native	GAAN
Galium aparine L. 1753	Rubiaceae	Native	GAAP
Nothofagus pumilio (Poeppig and Endl.) Krasser 1896	Fagaceae	Native	NOPU
Osmorhiza depauperata Phil. 1894	Apiaceae	Native	OSDE
Phleum alpinum L. 1753	Poaceae	Native	PHAL
Poa pratensis L. 1753	Poaceae	Exotic	POPR
Ranunculus biternatus Sm. 1814	Ranunculaceae	Native	RABI
Taraxacum officinale Weber 1780	Asteraceae	Exotic	TAOF
Trisetum spicatum (L.) K. Richter 1890	Poaceae	Native	TRSP
Uncinia lechleriana Steudel 1855	Cyperaceae	Native	UNLE
Viola magellanica Forster f. 1789	Violaceae	Native	VIMA
Introduced from *N. antarctica* forests			
Bromus unioloides Humb., Bonpl. and Kunth 1815	Poaceae	Native	BRUN
Calceolaria biflora Lam. 1785	Scrophulariaceae	Native	CABI
Cerastium arvense L. 1753	Caryophyllaceae	Native	CEAR
Cotula scariosa (Cass.) Franchet 1889	Asteraceae	Native	COSC
Deschampsia flexuosa (L.) Trin. 1836	Poaceae	Native	DEFL
Geum magellanicum Comm ex Pers. 1806	Rosaceae	Native	GEMA
Introduced from grasslands and peatlands			
Agoseris coronopifolium (D'urv) Chambers ex. D. M. Moore 1968	Asteraceae	Exotic	AGCO
Agrostis flavidula Steudel 1854	Poaceae	Native	AGFL
Alopecurus magellanicus Lam. 1791	Poaceae	Native	ALMA
Azorella lycopodioides Gaudich. 1825	Apiaceae	Native	AZLY
Capsella bursa-pastoris (L.) Medicus 1792	Cruciferae	Exotic	CABU
Chiliotrichum diffusum (Forster f.) O. Kuntze 1898	Asteraceae	Native	CHDI
Deschampsia antarctica Desv. 1853	Poaceae	Native	DEAN
Elymus agropyroides C. Presl 1830	Poaceae	Native	ELAG
Epilobium australe Poeppig & Hausskn. ex Hausskn. 1884	Onagraceae	Native	EPAU
Galium fuegianum Hooker f. 1847	Rubiaceae	Native	GAFU
Hieracium antarcticum D'Urv. 1825	Asteraceae	Native	HIAN
Hordeum comosum C. Presl 1830	Poaceae	Native	HOCO
Luzula alopecurus Desv. 1808	Cyperaceae	Native	LUAL
Osmorhiza chilensis Hookers and Arn 1833	Apiaceae	Native	OSCH
Phacelia secunda J. F. Gmelin 1791	Hydrophyllaceae	Native	PHSE
Phleum pratense L. 1753	Poaceae	Exotic	PHPR
Ranunculus peduncularis Sm. 1814	Ranunculaceae	Native	RAPE
Ribes magellanicum Poiret 1812	Saxifragaceae	Native	RIMA
Rubus geoides Sm. 1789	Rosaceae	Native	RUGE
Rumex acetosella L. 1753	Polygonaceae	Exotic	RUAC
Senecio vulgaris L. 1753	Asteraceae	Exotic	SEVU
Stellaria debilis D'Urv. 1825	Caryophyllaceae	Native	STDE
Stellaria media (L.) Vill. 1789	Caryophyllaceae	Exotic	STME
Veronica serpyllifolia L. 1753	Scrophulariaceae	Exotic	VESE

also includes deciduous trees (Linder et al., 1997). At a greater scale, it depends on continuous presence of the sensitive species on the landscape, variation in gap and tree-layer structure, availability of snags and dead wood of various sizes and decay stages, which are so-called old-growth qualities of a forest (Ohlson et al., 1997). Notice then that old-growth qualities could differ in different forests of the world, e.g., multi-specific overstory do not exist in old-growth *N. pumilio* forests.

4.3. Ecosystem management implications of variable retention

Several silvicultural methods based on natural regeneration of the natural forests have been proposed for southern Patagonia (Schmidt and Urzúa, 1982; Martínez Pastur et al., 1999b, 2000; Martínez Pastur and Lencinas, 2005; González et al., 2006; Rosenfeld et al., 2006). Initially, *Nothofagus* forests were harvested using clear-cuts (Gea et al., 2004), and then shelterwood cuts were

Appendix Table B
Mean occurrence frequency of understory plant species at the baseline and during the first 4 years after harvesting in *Nothofagus pumilio* forests (OGF = old-growth forests; DAR = combined (dispersed and aggregated) retention; DARI = combined retention inside aggregates; DARO = combined retention outside aggregates). Species codes figure in Appendix Table A.

	Baseline (2001)	OGF				DAR							
						DARI				DARO			
		2002	2003	2004	2005	2002	2003	2004	2005	2002	2003	2004	2005
Old growth *Nothofagus pumilio* forest species													
NOPU	1.00	1.00	1.00	1.00	0.70	1.00	1.00	1.00	0.75	1.00	1.00	1.25	1.00
OSDE	0.93	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.50	1.00
CAGL	0.93	1.00	0.90	0.90	0.90	1.00	1.00	1.00	0.50	1.00	0.83	1.50	0.67
GAAP	0.83	0.80	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.50	1.00
RABI	0.67	0.40	0.40	0.40	0.60	0.83	0.75	0.25	0.25	0.75	1.00	0.50	0.67
DYGL	0.63	<0.01	<0.01	<0.01	<0.01	<0.01	0.25	0.25	<0.01	<0.01	<0.01	0.50	0.50
UNLE	0.50	<0.01	0.20	0.20	0.30	<0.01	0.25	0.25	<0.01	0.25	<0.01	<0.01	<0.01
FEMA	0.33	0.80	0.90	0.60	0.60	0.33	0.50	0.25	0.25	0.50	0.50	0.25	0.50
VIMA	0.33		<0.01	0.20	<0.01								
POPR[a]	0.23	0.20	0.10	<0.01	0.10	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.33
PHAL	0.23	<0.01	0.10	0.10	0.30	<0.01	0.50	<0.01	<0.01	0.50	0.17	0.25	0.67
ACMA	0.20	<0.01	0.30	0.10	<0.01	<0.01	<0.01	<0.01	0.25	0.25	0.17	0.50	0.17
CYFR	0.20	<0.01	<0.01	<0.01	<0.01	<0.01	0.25	<0.01	<0.01		<0.01		0.17
TAOF[a]	0.17	0.20	0.40	<0.01	0.40	0.17	<0.01	<0.01	0.25	0.25	0.50	0.75	0.67
CEFO[a]	0.17	0.20	<0.01	<0.01	0.20	<0.01	0.25	<0.01	0.25	<0.01	0.17	1.00	0.50
TRSP	0.17	<0.01	0.30	0.30	0.20	0.33	<0.01	0.50	0.25	0.25	0.33	0.75	0.33
BEBU	0.10	0.20	<0.01	<0.01	<0.01	<0.01			<0.01	<0.01			0.17
GAAN	0.07		<0.01										
ADCH	0.07			<0.01									
ACOV	0.03		<0.01	<0.01	0.20			<0.01	<0.01			<0.01	<0.01
BLPE	<0.01	0.10	<0.01	<0.01	<0.01	<0.01		<0.01	<0.01	<0.01		<0.01	<0.01
Introduced from *N. antarctica* forests													
DEFL		<0.01	<0.01		0.10	<0.01	<0.01		0.25	0.25	0.17		0.33
BRUN		<0.01	<0.01	<0.01						0.25	<0.01	<0.01	0.33
CEAR		<0.01	<0.01	<0.01	<0.01					<0.01	<0.01	<0.01	<0.01
CABI		<0.01	<0.01	<0.01	<0.01								
GEMA		<0.01				7				<0.01	<0.01	<0.01	<0.01
COSC													<0.01
Introduced from grasslands and peatlands													
PHPR[a]				<0.01								<0.01	
CHDI				<0.01									
AGFL				<0.01									<0.01
DEAN				<0.01									
GAFU					0.10								
LUAL					0.10					<0.01	0.83		
PHSE					<0.01								<0.01
RIMA										<0.01			<0.01
RUAC[a]							<0.01	<0.01	0.25		<0.01	0.50	0.17
ELAG											<0.01	<0.01	<0.01
VESE[a]							0.25	<0.01				<0.01	<0.01
AGCO[a]													0.17
HOCO													<0.01
AZLY													<0.01
STME[a]													<0.01
CABU[a]													
SEVU[a]													
OSCH													
ALMA													
RAPE													
RUGE													
EPAU													
HIAN													
STDE													
Total species richness	21	21	25	27	25	18	17	19	21	22	22	23	33
Average species richness		24.5				18.75				25.0			
Exotic species richness	3	3	3	4	3	3	4	5	5	3	4	6	7

[a] Indicates exotic species.

recommended to improve re-growth (Schmidt and Urzúa, 1982; Martínez Pastur et al., 2000; Rosenfeld et al., 2006). But, this last method significantly affects the original diversity of *N. pumilio* forests (plants, mosses, birds, insects and mammals) (Martínez Pastur et al., 1999a, 2002; Pulido et al., 2000; Deferrari et al., 2001; Spagarino et al., 2001; Ducid et al., 2005). During the last 10 years, the variable retention approach has been proposed as a new and

more conservative harvesting alternative for these forests (Martínez Pastur and Lencinas, 2005; Lencinas et al., 2007; Martínez Pastur et al., 2009). It has been found to mostly conserve microclimatic and heterogeneity characteristics of the original forest structure (Martínez Pastur et al., 2010), while aggregated retention benefits birds (Lencinas et al., 2009) and moss conservation (Lencinas et al., 2008a). The variable retention silvicultural system is best suited for

Appendix Table C

Mean occurrence frequency of understory plant species at the baseline and during the first 4 years after harvesting in *Nothofagus pumilio* forests (DR = dispersed retention; AR = aggregated retention; ARI = aggregated retention inside aggregates; ARO = aggregated retention outside aggregates). Species codes figure in Appendix Table A.

| | Baseline (2001) | DR | | | | AR | | | | | | | |
| | | | | | | ARI | | | | ARO | | | |
		2002	2003	2004	2005	2002	2003	2004	2005	2002	2003	2004	2005
Old growth *Nothofagus pumilio* forest species													
NOPU	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00	1.00	0.57	0.86	0.43
OSDE	0.93	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
CAGL	0.93	0.90	1.00	0.90	0.50	1.00	1.00	1.00	0.67	1.00	1.00	1.00	0.57
GAAP	0.83	0.70	0.80	1.00	1.00	1.00	0.67	1.00	0.67	0.71	0.57	0.71	1.00
RABI	0.67	0.50	0.50	0.60	0.40	1.00	1.00	1.00	0.67	0.86	0.43	1.00	0.71
DYGL	0.63	<0.01	<0.01	0.10	<0.01	0.33	0.33	<0.01	0.33	0.29	<0.01	0.29	0.57
UNLE	0.50	0.10	0.10	0.60	<0.01	0.67	0.33	0.67	0.67	0.57	<0.01	0.14	0.43
FEMA	0.33	1.00	0.90	0.90	0.80	0.67	0.67	1.00	0.67	0.43	0.57	0.71	0.29
VIMA	0.33					<0.01			<0.01	<0.01			0.14
POPR[a]	0.23	<0.01	0.10	<0.01	<0.01		<0.01	0.33	<0.01		<0.01	0.14	0.57
PHAL	0.23	0.30	0.20	0.40	0.40	0.33	<0.01	<0.01	<0.01	0.57	0.14	0.43	0.71
ACMA	0.20	<0.01	<0.01	0.20	0.20	0.33	<0.01	<0.01	<0.01	0.29	<0.01	0.14	0.43
CYFR	0.20	<0.01	<0.01	<0.01	<0.01	<0.01	0.33	<0.01	0.33	<0.01	0.14	<0.01	0.14
TAOF[a]	0.17	0.20	0.70	0.50	0.50	0.33	<0.01	0.33	<0.01	0.29	0.57	0.43	0.71
CEFO[a]	0.17	0.10	0.10	0.10	0.20	0.33	<0.01	0.33	<0.01	0.14	0.29	0.57	0.86
TRSP	0.17	0.30	0.50	0.20	0.40	0.33	0.33	0.33	0.33	0.43	<0.01	0.29	0.29
BEBU	0.10	0.10	<0.01	<0.01	<0.01	<0.01				0.14	<0.01	<0.01	<0.01
GAAN	0.07					<0.01							
ADCH	0.07					<0.01				0.29			
ACOV	0.03			0.10	<0.01		<0.01	<0.01	<0.01		<0.01	<0.01	<0.01
BLPE	<0.01			<0.01	<0.01	<0.01			0.33	0.14			0.29
Introduced from *N. antarctica* forests													
DEFL		<0.01	0.40		0.50	<0.01	<0.01	0.33	<0.01	<0.01	<0.01	0.29	0.14
BRUN			<0.01	<0.01	0.10					0.14	<0.01	<0.01	0.29
CEAR			<0.01	<0.01	<0.01						<0.01	<0.01	<0.01
CABI				<0.01	<0.01							<0.01	
GEMA			<0.01	<0.01	0.10	0.33	<0.01	<0.01	<0.01	<0.01	0.14	0.14	<0.01
COSC			<0.01	<0.01						0.14		<0.01	<0.01
Introduced from grasslands and peatlands													
PHPR[a]			<0.01	<0.01									
CHDI			<0.01		<0.01								
AGFL			<0.01		<0.01					0.29		0.29	0.29
DEAN													<0.01
GAFU												<0.01	<0.01
LUAL				<0.01									
PHSE			<0.01		<0.01							<0.01	<0.01
RIMA				0.10	<0.01					<0.01	<0.01	<0.01	0.29
RUAC[a]		<0.01	<0.01	<0.01	0.30					0.14	<0.01	<0.01	0.57
ELAG			<0.01	<0.01	<0.01					<0.01		<0.01	0.29
VESE[a]				<0.01	<0.01					0.14	<0.01	0.14	0.14
AGCO[a]					<0.01								
HOCO				<0.01	<0.01							<0.01	<0.01
AZLY					<0.01								<0.01
STME[a]											<0.01		<0.01
CABU[a]			<0.01	<0.01	<0.01					<0.01	<0.01		0.14
SEVU[a]			<0.01	<0.01	<0.01								<0.01
OSCH					<0.01								<0.01
ALMA					<0.01								<0.01
RAPE					<0.01								
RUGE					<0.01								
EPAU										<0.01			<0.01
HIAN											<0.01	<0.01	
STDE											<0.01		<0.01
Total species richness	21	18	28	32	39	21	18	18	20	29	28	32	41
Average species richness		29.25				19.25				32.5			
Exotic species richness	3	4	7	8	8	2	3	3	3	5	7	5	8

[a] Indicates exotic species.

areas where timber production is desired but maintenance of the structural complexity and biological legacies found in older forests is as important as, or even supersedes, yield and improvement of growing stock (Mitchell and Beese, 2002).

Different patterns and levels of variable retention produce diverse resistance to harvesting impacts on understory diversity in *Nothofagus* forests. Dispersed retention is believed to be most appropriate where ecological objectives require target structures or conditions to be uniformly distributed, such as supply of downed woody debris and snags, or mitigating microclimatic or hydrologic impacts. However, in southern Patagonia, dispersed retention is comparable to shelterwood cuts when a final intervention is not applied, which is clearly shown in the similarity between DARO and DR in the multivariate analyses. Then, dispersed retention impacts on *Nothofagus* forest biodiversity would probably be the same than in shelterwood harvested stands. On the other hand, aggregated retention is expected to be more effective in maintaining a broader array of structural elements and ecological conditions, resembling old-growth characteristics into the harvested stands. Old-growth forests are less dynamic, but more structurally complex than harvested stands. Environmental heterogeneity and interspecific microhabitat preservation are thus important for the maintenance of local species diversity in the forest understory, not only for common species but also for infrequent species or functional groups.

Aggregated and dispersed combined systems, as DAR, imply less impact at the whole stand level because benefits of both retention patterns are achieved, such as the fact that less changes in understory cover, biomass and richness were observed in DAR than in pure treatments (AR or DR), as well as only a minor level of species introductions. On the other hand, no harvesting of associated environments or key habitats (Gustafsson et al., 2010) creates retention patches in managed landscapes, but their structural and functional characteristics greatly differ from old-growth timber quality stands in southern Patagonian forests (see Lencinas et al., 2005, 2008b, 2008c). So, only aggregates could conserve old-growth qualities and particular habitat characteristics present in timber quality stands. Managing landscapes for a greater range of habitat conditions may, therefore, be essential for some organisms (Mitchell and Beese, 2002) such as insect communities (Lencinas et al., 2008c).

It is important to point that that contrary to most of the other temperate timber forests found around the world, Tierra del Fuego's pure *N. pumilio* forests are mainly old-growth and have never been harvested in the past. In forests with a long history of intensive management, like European temperate forests, species intolerant to changes in environmental conditions generated by forest management could be already extinct and greater homogenization in forest structure could exist due to repeated cycles of intensive harvesting. This could be an explanation of the lack of differences between specific composition of new and old forests in some European studies (Graae and Sunde, 2000), as well as the low benefits of variable retention treatments on their understory conservation (Vanha-Majamaa and Jalonen, 2001). Variable retention improvements in southern Patagonian *Nothofagus* forests could be enhanced due to the old-growth pristine condition, not only in composition but also in structure and habitat diversity. However, in secondary forests regenerated in natural impacted large areas, including windthrow or avalanche areas, variable retention management could preserve patches that will resemble old-growth forest characteristics in less time than other harvesting techniques. Moreover, retention patches must be left in an un-harvested state for more than one cycle of forest management, allowing long-term recovery of habitat and species diversity in both historically harvested and old-growth forests.

Appendix

See Appendix Tables A–C.

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