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Moderate-severity silvicultural methods generate better forest reorganization than other silvicultural methods in temperate rainforests four decades after implementation

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ABSTRACT

Silvicultural regeneration methods promote regeneration of new tree cohorts following the harvest of mature trees and include a gradient of options from cutting all (clearcuts) or some (selection cuts) trees resulting in even- or uneven-aged forests. For forest managers and landowners, it is essential to have the best possible information on how forests reorganize following these different methods. Forest development, composition and growth are dependent on site quality and harvest type. In this study we evaluated two even-aged (clearcut (CC), seed-tree cut (STC)), one two-aged cut (extended irregular shelterwood (ISC)), one uneven-aged (single-tree selection cut (SC)), and an unmanaged control (CON), four decades after harvest implementation in old-growth Evergreen temperate rainforests above 500 m a.s.l. in the Coastal Range of south-central Chile. These forests grow on poor-quality sites due to old and shallow soil conditions and were dominated by late-successional species and a thick understory with the bamboo *Chusquea machrostachya* at the time of harvest implementation. Compositional and structural conditions reflected the type of harvests, with even- and two-aged methods largely similar to one another and the SC and the OG having very similar characteristics, which is likely a consequence of the very light severity of the SC. Tree species composition in even-aged harvests was dominated by shade midtolerant species of high timber value, although short-lived pioneer species of the Proteaceae family were also abundant, especially in ISC. The ISC had the greatest homogeneity in all stand variables (tree density, basal area, volume, and quadratic stand diameter), and since it was a two-layered forest, had basal areas and volumes close to the SC and OG, and a rotated-sigmoid diameter distribution (different to all other treatments). Height of the new cohort in the ISC was significantly taller than in the CC and the STC for most species' groups, suggesting that the cut plus the residual canopy of ISC diminished the initial cover of the bamboo *C. macrostachya* and competition for regeneration. Only diameter growth of trees of all shade tolerances was lower in ISC, but diameter growth patterns were similar to CC and STC, with increasing growth during the first two-three decades followed by a decline. Based on these findings, we conclude that silvicultural methods of intermediate harvesting severity, especially ISC, provide the best ecological and economic option in these poor-quality sites given rapid reorganization following their implementation, while maintaining a relatively complex vertical structure, high tree species diversity, and a growing stock dominated by tree species of high timber value.

1. Introduction

Silviculture plays a key conservation role in highly forested regions and is tightly linked to local cultures and economies (Sivadas, 2022). Tree harvesting and land-use changes are usually the main pressures upon these forests (Miles and Kapos, 2008). Therefore, a key path to forest conservation in private lands often depends on management practices that provide desirable values to landowners (maintenance of

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species of high economic or cultural value) while also maintaining essential forest attributes (composition, structure and function; Perry, 2008) for the provision of different ecosystem services (Felipe-Lucia et al. 2018). Many of the conditions providing these diverse ecosystem services are found in mature and old-growth forests, which has been recognized by a growing interest in silvicultural strategies to restore and maintain these conditions (Bauhus et al. 2009) In this context, the long-term evaluation of forest characteristics such as regeneration, growth, structure and composition resulting from different silvicultural methods, as well as in comparison with old-growth forests, is fundamental to determining the silvicultural strategies that best balance and sustain ecological and economic objectives for a given territory and forest type.

In general, uneven-aged silvicultural systems are often recognized as providing sustained incomes of high-quality timber from periodic harvests (e.g., O'Hara, 2015, Nyland, 2016), compared to lower incomes from even-aged systems. Some long-term evaluations of forest development following regeneration cuts seem to confirm this. For instance, in temperate forests in the northern hemisphere, Niese and Strong (1992) determined that after 40 years of management, moderate severity selection systems delivered the best combination of species diversity and economic returns among the uneven-aged cuts, while the shelterwood system was the best among even-aged cuts. Similarly, Draper et al. (2021) determined that after 50 years selection treatments removing more basal area provided an overall better return on investment. Long-term evaluation (> 50 yr) aimed at identifying tradeoffs between the achievement of mitigation and adaptation objectives suggest that a potential stand-level strategy for balancing these goals may be to employ multi-aged management systems, such as irregular shelterwood and selection systems (D'Amato et al., 2011). In spite of the general advantages perceived for uneven-aged silviculture, Nolet et al. (2018) conducted a meta-analysis that included a large range of indicators and many different taxonomic groups, and found that neither uneven- or even-aged silvicultural approaches can ensure a greater number of positive impacts upon these indicators, and that both are needed in the landscape in conjunction with protected areas, especially for the conservation of taxonomic diversity.

In the case of Valdivian temperate rainforests (VTR; Veblen and Alaback, 1995) in south-central Chile, which are dominated by high timber value mixed hardwoods (Loguercio et al., 2018, Donoso et al. 2022, Donoso and Navarro, 2022), there are only few long-term silvicultural experiments examining regeneration cuts. Forests in this region include mostly the Evergreen forest type (one of the largest in the country with 3,5 million ha), and the Roble-Raulí-Coihue forest type (1, 7 million ha) (CONAF, 2021). In the early 1980 s, Donoso (1989a) established a long-term study of regeneration cutting methods in forests of the Coastal and Andean Evergreen Forest, and three years after the cuts determined very high numbers of seedlings across a range of methods, although in greater numbers and more homogeneously distributed in the Andes. For the even-aged methods in these cuts in the Andes (clear cut in blocks and strips, plus extended shelterwood cut), Donoso et al. (2019) showed that these forests had similar high tree numbers and stocking (but lower in the shelterwood cut) in a diversity of tree species 26 years after the cuts, although with a dominance by the short-lived *Embothrium coccineum* (Proteaceae; a pioneer and very shade intolerant tree species). Recent evaluations over shorter periods (< 10 yr) with different silvicultural approaches have also occurred. For example, Schnabel et al. (2017) reported that single-tree selection harvests did not affect plant diversity but partially affected height and diameter structure compared to old-growth forests, and Donoso et al. (2020) reported high tree regeneration numbers and good growth rates for selection forests. Other than this, early results of variable-density thinning in two types of secondary forests managed to increase regeneration and other attributes common in old-growth forests have shown high regeneration numbers and diameter growth among residual trees (Donoso et al. 2020). These variable-density thinning cuttings have resulted in high incomes from the timber and the firewood produced (e.g. Donoso et al. 2014). Estimates by Nahuelhual et al. (2007) provide positive results for uneven-aged silviculture, but comparisons with even-aged cuts were not made.

The scarcity of long-term evaluations of different silvicultural treatments in the VTR region (or in any region) limits the level of information for generating sound management decisions over time. In that context, we sought to evaluate the silvicultural experiments established by Donoso (1989a) many decades ago in the west slope of the Coastal Range. The experiment included even-aged silvicultural methods (clear cut, seed-tree cut and shelterwood cut), and an uneven-age method (very low-severity selection cut), and control plots in an area of old-growth forests with no previous human disturbances. However, in the case of the shelterwood cut there was never a final cut, so it can be considered an extended irregular shelterwood method (Raymond et al. 2009). By age three there were huge numbers of seedlings in these experiments, but there were no further additional publications about composition, regeneration, and growth. Here we sought to evaluate this experiment after four decades since its implementation. After three years of evaluation, Donoso (1989a) indicated that the seed-tree, uniform shelterwood and single-tree or group selection were not technically or economically efficient or advisable in the previously unmanaged evergreen forest type. The clear-cut method was not recommended either, unless it was applied in strips or on small areas. Instead, Donoso (1989a) suggested that some variant of the shelterwood method be applied to regenerate and establish shade-tolerant species. On average, however, the midtolerant species *Eucryphia cordifolia* (a hardwood tree species of high timber value and vigorous vegetative regeneration through root sprouts (Escandon et al. 2013)) represented one of the promising species according to its density and growth.

For the Evergreen Forest Type, forest productivity is much lower in the Coastal vs. the Andean Range (Donoso, 1989b) . Even within the Coastal Range, the west- and the east-facing slopes are different in their soil characteristics, especially because soils in the east-facing slopes include fine-texture volcanic materials and are deeper (Donoso, 2005). Overall, the west-facing slope of the Coastal Range, especially at mid- to high-elevations (> 500 m a.s.l.) are among the poorest sites for forest growth in the region (Donoso and Navarro, 2022). In addition, these forests are difficult to manage since they have vigorous understories dominated by the bamboo *Chusquea machrostachya*. and the fern *Lophosoria quadripinnata* (Donoso and Nyland, 2005). The combination of slow-growing trees in these poor sites and the competition by bamboos and ferns makes the regeneration process a significant challenge for foresters and landowners (Donoso 1989b). Given these ecological conditions, we hypothesized that a silvicultural method of intermediate harvest severity could deliver the best combination of tree species composition, regeneration and growth in the long term, in line with aspects of the patterns predicted by the Intermediate Disturbance Hypothesis (Grime, 1973, Connell, 1977). Therefore, our main objective was to evaluate which silvicultural methods had achieved better tree composition (in terms of long-lived tree species of high timber value) and growth after four decades of development without any tending (e.g. thinning), while also sustaining aspects of structural conditions found in old-growth forests of this type. Results may contribute to supporting management of these Coastal forests that without management or when mismanaged are perceived to have a low economic value to landowners.

2. Methods

2.1. Study area

In 1982, the Universidad Austral de Chile, in partnership with the National Forestry Corporation (CONAF), conducted an experiment on silvicultural methods in the Coastal Mountain Range of the Los Ríos Region (40° 10'S - 73° 36' W), at slopes <30% between 520 and 610 m above sea level. The area has a rainy temperate climate with

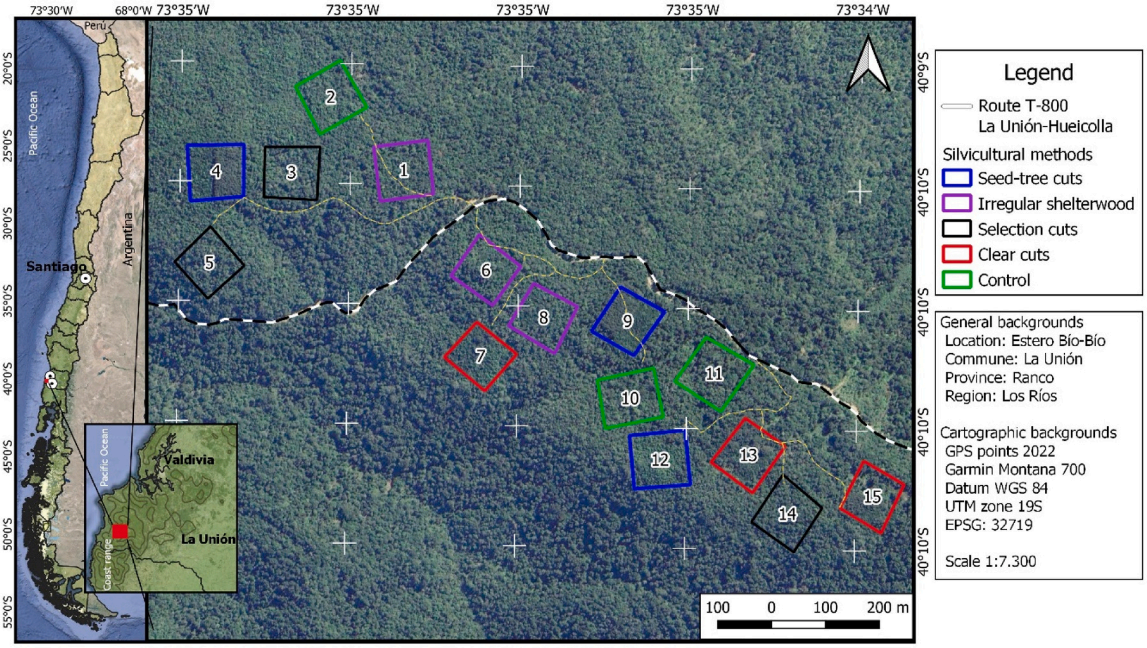

Fig. 1. Distribution of the study plots in the study area. Plots that were harvested with more intense methods (clear cuts and seed tree cuts) can still be distinguished in the aerial photo. Inset figures show the general location of the study area.

precipitation mostly in the form of rain. According to Donoso (1989a), the annual precipitation in the study area can reach 4000 mm, with a clear decrease in the summer months. Measurements by Marchant (1984) along all seasons in a clearcut and in a selection plot in the study area during 1982–1983 actually exceeded these values with 4793 and 4376 mm of precipitation occurring in these plots (10% in summer, 25% in fall, 40% in winter and 25% in spring). The average annual temperature is 11.9°C. The soils in the Coastal Mountain Range belong to the Hueicolla series, developed *in situ* on residual metamorphic material of the mica-schist type (CIREN, 2001). Soils are acidic, poorly drained, and moderately deep and are of low to medium productivity ((Donoso, 1989a, Donoso, 2005, Donoso and Navarro, 2022). Most remaining Evergreen forests are largely restricted to higher elevations, since they have been replaced by agriculture fields or forest plantations of exotic species at lower elevations.

Based on the initial inventory of the 15 plots in the experiment (Donoso, 1989a), the forest had an average of 684 trees per hectare $\geq$ 5 cm in diameter at breast height (dbh) and 102 m^2 per hectare in basal area prior to harvesting. *Laureliopsis philippiana*, *Saxegothaea conspicua*, and *Amomyrtus luma* were the species with the highest importance values based in tree density and basal area (24%, 20%, and 19%, respectively), while other species that achieved importance values above 5% corresponded to *Eucryphia cordifolia*, *Dassiphyllum diacanthoides*, and *Gevuina avellana*. Forest species with lower importance included *Drimys winteri*, *Aextoxicon punctatum*, and *Weinmannia trichosperma*, among others. No harvesting or management had occurred in these forests prior to the establishment of the experiment.

2.2. *Experimental design and field procedures*

This experiment was established using a completely randomized experimental design with three 1-hectare plots randomly distributed to each of four different silvicultural methods or regeneration cuts: clearcutting (CC), seed tree (10–15 residual trees per hectare; STC), shelterwood (50% of residual basal area; ISC) and selection (80% of residual basal area; SC). An equal number of control plots were also established in the old-growth that surrounds the experiment (CON; Fig. 1). This design originally included the implementation of three different even-aged silvicultural methods and one uneven-aged method (selection); however, the shelterwood cut never had a final overstory removal cut, so it became a reserve shelterwood method (Nyland, 2010), or an extended irregular shelterwood (Raymond et al. 2009). A similar dynamic occurred in an analogous experiment in the Andes in which the final overstory removal cut of the regular shelterwood method was not implemented either, with no stipulation for the final removal cut in the first report of this experiment (Donoso, 1989a). On the other hand, the selection cut consisted primarily of the harvest of a few large-sized trees, without tending the intermediate diameter classes, so it was a light cut and did not fulfill the requirements of a truly implemented selection system (*sensu* Nyland, 2016). Harvesting was conducted with chainsaws and wood was transported to the log landings, close to the plots, with oxen. In the managed plots there were no further interventions, such as tending operations in the even- and two-aged cuts or new entries following cutting cycles in the selection cuts.

In the summers of 2022 and 2023 we established and measured sampling plots within the original 1-ha plots. These sampling plots ranged from 1800 to 2400 m^2 in size (60×40 or 60×30 m) and are consistent with plot sizes suggested by Curtis and Marshall (2005), which suggest that plots must have a size proportional to the mean size of trees, sizes up to 0.2 ha (2000 m^2), and at least 100 trees. Our plots satisfy all these requirements.

In each sampling plot all tree, small tree, and shrub species with a diameter at breast height (dbh) $\geq$ 5 cm were measured. Each individual was recorded with its species and dbh, following the protocols of forest inventories by Prodan et al. (1997). In addition, in each sampling plot within the CC, STC and ISC treatment, total height was measured for approximately 20 dominant individuals of form and health class 1 belonging to the post-harvest regeneration cohorts. Volumes were estimated with functions provided by Drake et al. (2003) and Donoso et al. (2020).

Increment cores were extracted for the measurement of growth in dbh and age of each of the trees selected for height measurement for the CC, STC and ISC. For SC and CON we also obtained increment cores from approximately 20 dominant healthy and well-formed trees per plot, with the aim of obtaining growth over the last 40 years (but not age of the trees). Each core was mounted following standard procedures of Stokes

Table 1
Pre- and post-harvest descriptive statistics for each treatment and control. CC: Clear cut; STC: Seed-tree cut; ISC: Irregular shelterwood cut; SC: Selection cut; CON: Control.

Treat.	Slope range (%)	Tree density		Basal area (m^2)		Volume (m^3)		QSD (cm)	
		Pre-H	Post-H	Pre-H	Post-H	Pre-H	Post-H	Pre-H	Post-H
CC	6–14	681± 393	0 ± 0	78,7 ± 0	0,0 ± 0	389,2 ± 68	0,0 ±0	38,5±2,1	0,0±0,0
STC	5–10	882±379	13±2	91,6±0,5	6,9±0,5	457,0±116,1	42,9±8,7	38,0±6,9	83,3±5,7
ISC	5–20	865±98	212±42	101,4±6,4	44,2±6,4	447,0±16,8	220,1±42,0	38,7±3,2	51,7±2,1
SC	9–12	1082±375	900±241	106,9±14,6	80,2±14,6	508,6±21,4	377,7±76,0	36,7±6,1	34,3±6,4
CON	12–25	1039±600	1054±588	86,4±20,8	87,7±20,8	398,6±138,0	370,1±128,7	36,0±14,5	36,0±14,1

and Smiley (1968). After drying, the extracted and mounted cores were polished in the transverse plane of the wood with an orbital sander, starting with coarse-grained sandpaper (100 grains per cm^2) and ending with finer-grained sandpaper (500 g per cm^2) to visually distinguish the boundaries of the rings. The samples were scanned with an Epson Expression 11000XL scanner, Itrax version at 1200 DPI, calibrated to recognize distances in images. The width of the rings was measured with the CooRecorder software version 7.6 (Larsson, 2013). Since the samples were collected in the summer of 2021 and the last growing season in the southern hemisphere began in the spring of 2020, the last ring formed (the one closest to the bark) was dated as 2020 following the convention of Schulman (1956).

In each sampling unit, a 2 m^2 plot was systematically measured for every 50 m^2 quadrats (10 ×5 m) of the unit to quantify regeneration, including seedlings (< 200 cm in height) and saplings (≥ 200 cm in height and < 5 cm in dbh) according to species and height. The cover of non-arboreal vascular species of the understory was estimated in 1 m^2 within these plots; however, only the cover for two strong competitors of tree species, the bamboo *Chusquea macrostachya* and the fern *Lophosoria quadipinnata* (see Donoso and Nyland, 2005), are presented for this work.

Table 2
Mean and standard deviation for different structural variables with per-ha values by silvicultural cut and for the old-growth forests. Treatments with different letters are significantly different for a given variable. QSD: quadratic stand diameter, or the diameter of the tree with average basal area; CC: Clear cut; STC: Shelterwood cut; ISC: Irregular shelterwood cut; SC: Selection cut; CON: Control.

Variable	CC	STC	ISC	SC	CON
Total tree densityNew cohort*	3747 ±2448 ab3747 ±2448 a	6565 ±1054 a6543 ±1050 a	4165±543 ab4033 ±556 a	1331 ±90 b-	1430 ±725 b-
Total basal area (m^2)New cohort*	39±26 b39 ±26 a	56±8 ab50 ±7 a	74±2 ab34±5 a	86±20 a-	86±5 a-
Total volume (m^3)New cohort*	197±144 b197±144 a	258±3 ab216±33 a	404±7 ab150±25 a	500 ±154 a-	511 ±104 a-
Total QSD (cm) New cohort*	11.6±0.7 b11.6±0.7 a	10.4±0.1 b9.9±0.5 b	15.1±1.0 b10.3±0.1 b	28.6 ±4.3 a-	29.7 ±8.3 a-

[*] New cohort corresponds to trees below 30 cm in dbh for CC, STC and ISC.

2.3. Analyses

The analysis for species importance among harvesting treatments was first conducted by determining the importance values-IV, based on relative tree numbers and basal area of each species with dbh ≥ 5 cm in relation to total tree density and basal area, according to Curtis and Mclntosh (1951). Using the IV per species and plot level we conducted the blocked distance-based multivariable analysis of variance (PERMANOVA; (Anderson and Walsh, 2013)) to test if treatments as factor differed. To do so, the adonis function in Vegan package in R was used. Specifically, the pairwise multi-response permutation procedure used the Bray-Curtis distance measure based on 999 permutations and median alignment within treatment to mitigate the impact of large values (Anderson and Walsh, 2013). Statistical significance among treatments was determined at $\alpha = 0.05$ and the betadisper2 function in Vegan package (an analogue to the Levene's test) confirmed the assumption of homogeneity of variances. To visualize the treatments, nonmetric multidimensional scaling (NMDS; Kenkel and Orloci, 1986) was used with the metaMDS function in Vegan package in R (Oksanen et al. 2022). The final ordination solution for overstory plants was rotated to align the gradient of harvesting severity represented by treatments along the first NMDS axis. Species composition in the five treatments were analyzed by indicator species analysis for individuals with dbh ≥ 5 cm, to detect specificity of woody plants to different severity of treatment at the species level. "Indicspecies" package of R was used for Indicator species analysis (Cáceres et al., 2020). The dependent variable was the species abundance matrix of woody plants, considering those with a significant p-value below 0.05 as indicator species of each group.

Analysis of diameter distribution shapes was based on the methods of Janowiak et al. (2008) and Alessandrini et al. (2011). Thus, a logarithmic scale was used for density and polynomials up to the third order were fit to the diameter distribution of each treatment using ordinary least squares. The best significant ($p < 0.05$) model among all possible combinations was selected using the Akaike Information Criterion (Akaike, 1974). Adjusted coefficient of determination (adj. R^2) and root mean square error (RMSE) were then computed for the selected model. The diameter distribution shape was named according to the terminology used in Table 2 of Janowiak et al. (2008). All analysis was done in the R software environment (R Development Core Team, 2021).

Differences in structural variables (tree density, basal area, volume and quadratic stand diameter (QSD)) at the stand or treatment level were compared using analysis of variance (ANOVA), for all individuals $\geq$ 5 cm in dbh, by species and according to shade tolerance groups (functional groups), which included: long-lived shade-intolerant species, short-lived shade-intolerant species, midtolerant species, canopy shade-tolerant species, and understory shade-tolerant species (or lower canopy species that include trees and some shrubs). Similarly, differences in growth in dbh between silvicultural methods were compared using ANOVA, by species and according to shade tolerance groups (functional groups). Special attention was given to comparison of differences in periodic annual increment (PAI) and mean annual increment (MAI) by tree species, functional groups and for the average of the species with dominant positions in the cohort regenerating after implementation of the silvicultural methods. In all cases, differences between treatments were considered significant when the probability value was < 0.05. When significant differences were detected, the Tukey HSD test was run to identify which groups were different.

Regeneration densities were compared between treatments according to species' shade tolerances, using ANOVA. To consider the hierarchical structure of the data (plots nested within treatments), mixed effects models were fitted by adding random effects at the plot level. The models were fitted using maximum likelihood (Pinheiro and Bates, 2000). Differences between treatments were considered significant when the probability value was < 0.05. When significant differences

Table 3
Importance value (IV) for the three main species per shade tolerance groups. For all treatments these nine species sum 80–90% of the IV.

	Shade-intolerant species			Midtolerant species			Shade-tolerant species		
Treatment	em[*]	lf	ga	ec	dw	dd	lp	sc	al
CC	7,5	4,8	5,2	25,6	10,0	13,6	1,0	1,7	17,8
STC	5,1	7,9	4,5	15,9	11,7	14,0	0,8	3,1	26,3
ISC	0,2	18,1	10,9	9,0	3,9	8,0	9,8	7,3	16,2
SC	0,3	6,5	4,5	4,2	5,2	7,1	25,3	18,3	16,4
CON	0,0	2,2	5,2	4,0	12,6	7,2	17,8	17,2	15,6

[*] em: Embothrium coccineum; lf: Lomatia ferruginea; ga: Gevuina avellana; ec: Eucryphia cordifolia; dw: Drimys winteri; dd: Dasyfhyllum diacanthoides; lp: Laureliopsis philippiana; sc: Saxegothaea conspicua; al: Amomyrtus luma.

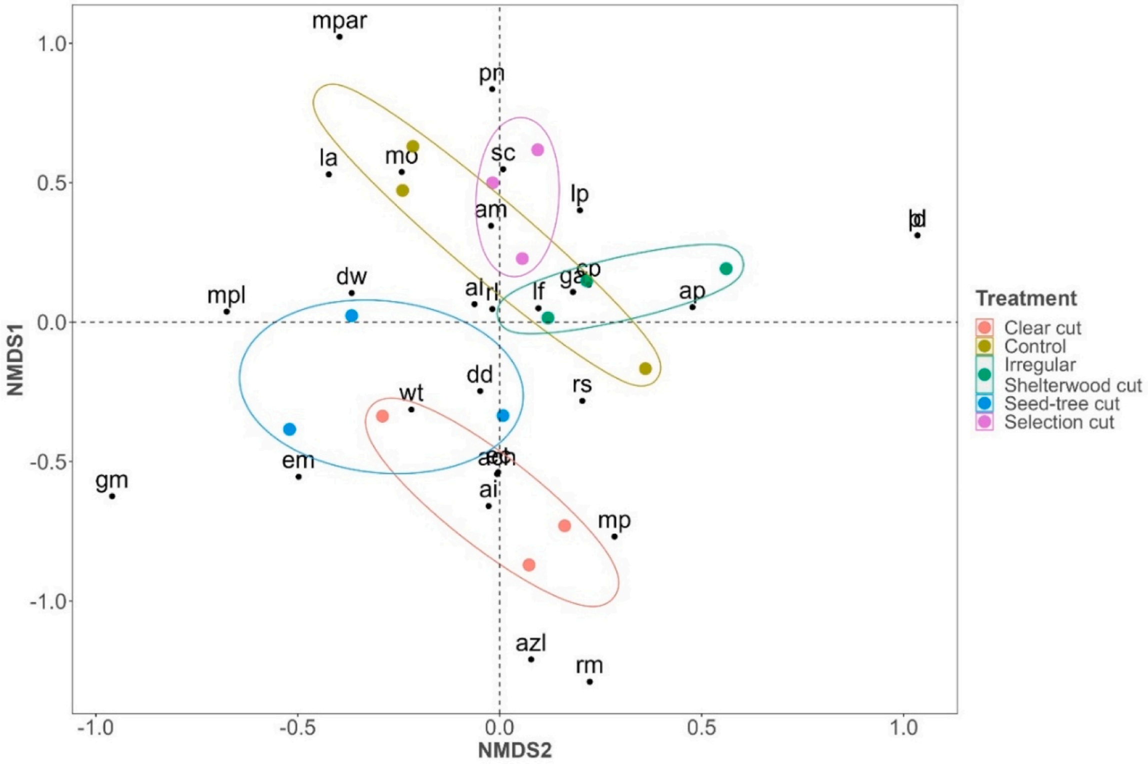

Fig. 2. Non-metric multidimensional scaling (NMDS) ordinations of overstory plants for each silviculture treatment (Clear-cut, Seed-tree cut, Irregular Shelterwood cut, Selection cut and Control). Ordination diagrams were rotated to represent the gradient of disturbance clearly associated to each treatment and the variability of species composition. The letters inside the plot are the tree species, as follows: ach = *Aristotelia chilensis* (Molina) Stuntz; ai = *Azara integrifolia* Ruiz & Pav.; al = *Amomyrtus luma* (Molina) D. Legrand & Kausel; am = *Amomyrtus meli* (Molina) D. Legrand & Krausel; ap = *Aextoxicon punctatum* Ruiz & Pav.; azl = *Azara lanceolata* (Lam.) Hook. F.; cp = *Caldcluvia paniculata* Cav. (D. Don); dd = *Dasyphyllum diacanthoides* (Less.) Cabrera; dw = *Drimys winteri* J.R.Forst. & G.Forst.; ec = *Eucryphia cordifolia* Cav.; em = *Embothrium coccineum* J.R.Forst. & G.Forst.; ga = *Gevuina avellana* Molina; lp = *Laureliopsis philippiana* (Looser) Schodde; ld = *Lomatia dentata* (Ruiz & Pav.) R.Br.; lf = *Lomatia ferruginea* (Cav.) R.Br.; la = *Luma apiculata* (DC.) Burret; mo = *Myrceugenia ovata* (Phil.) L.E. Navas; mpar = *Myrceugenia parviflora* (DC.) Kausel; mp = *Myrceugenia planipes* (Hook. & Arn.) O.Berg; pl = *Persea lingue* (Ruiz & Pav.) Nees; pn = *Podocarpus nubigena* Lindl.; rl = *Raukaua laetevirens* (Gay) Frodin; rm = *Ribes magellanicum* Poiret; rs = *Rhaphithamnus spinosus* (Juss.) Moldenke; sc = *Saxegothaea conspicua* Lindl.; wt = *Weinmannia trichosperma* Cav.

were detected, the Tukey HSD test was run to identify which groups were different.

3. Results

3.1. General description of the forests

The two even-aged methods (CC, STC) and the two-aged method (ISC) had high tree densities, which were not significantly different among them due to the high variability (standard deviation) of the CC plots (STC had 75% higher tree density than CC) (Table 2). For the same reason, these three treatments did not significantly differ for basal area, volume and quadratic stand diameter (QSD) for all trees, and only differed for a higher QSD of the new cohort in the case of CC. The new cohort in STC had between 20% and 30% more basal area, and between 10% and 30% more volume than CC and ISC, but those differences were not significant ($p>0.05$). Tree density was greater in the even-aged methods (CC, STC) and the two-aged method (ISC) compared with the SC or the control forest (OG). Basal area was greater for the SC and OG. ISC had the highest basal area among the even- and two-aged methods and was close to SC and OG largely due to basal area retained in canopy trees following the initial seed cut. Mean annual increment in volume for the new cohorts ranged between 3.8 and 5.4 m^3 for these cuts.

Only STC significantly differed from SC and OG in tree densities ($p<0.05$). Basal area and volume increased from CC through SC and OG (which had the same basal area), and only CC differed significantly from SC and OG. The quadratic stand diameter (QSD) was lower for CC and STC, intermediate for ISC, and higher for SC and OG, and significantly different ($p<0.05$) between the even-aged cuts and SC and OG, which did not differ from one another ($p>0.05$). The SC and OG had similarly

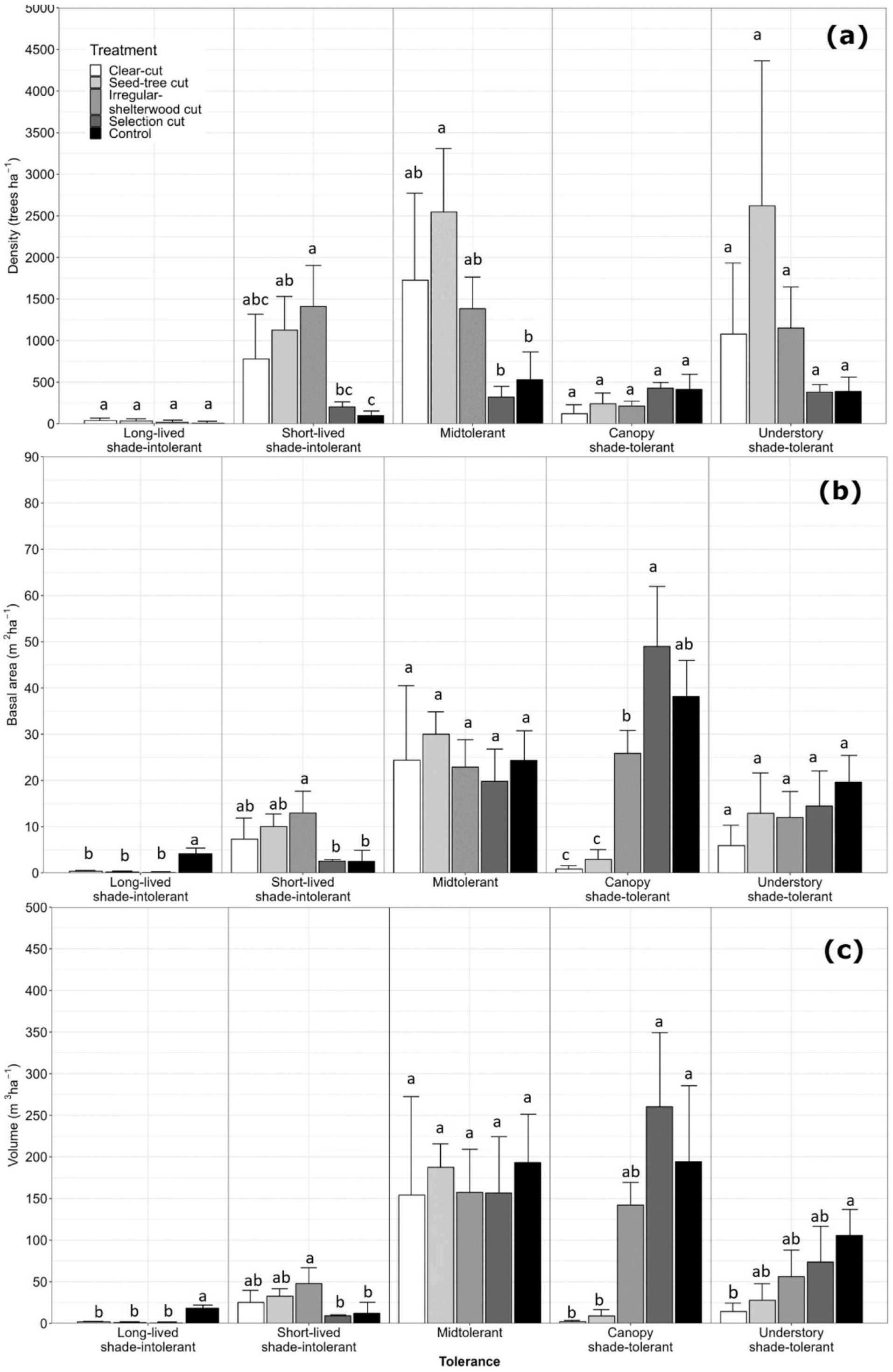

Fig. 3. Stand structural variables four decades after the implementation of silvicultural methods and for the control forest by shade tolerance/longevity functional groups ((a) Tree density, (b) Basal area, (c) Volume)). Different letters between treatments within each panel represent statistically significant differences between treatments ($p < 0{,}05$).

low numbers of trees and high basal areas and volumes (Table 2).

3.2. Composition of tree and arborescent species

Species shown in Table 3 jointly comprise more than 80% of the importance value for each treatment. Table 3 also reflects the dominance of mid-tolerant species in CC and STC (especially *E. cordifolia*), of short-lived shade-intolerant species in ISC (especially *L. ferruginea*) and of shade-tolerant species in SC and OG (especially *L philippiana*). The shade-tolerant *A. luma* had high importance value in all treatments.

The PERMANOVA showed significant differences in IV among treatments sites ($F = 3.911$, $p < 0.001$). There were three significant pairwise comparisons: CC and the SC treatment ($F=1.127$; $p=0.01$), CC and OG ($F = 4.821$; $P=0.014$), and between STC and SC ($F=6.089$; $p=0.011$). CC and ISC were marginally different ($F=4.693$; $P=0.06$). The NMDS ordination for species with dbh $\geq$ 5 cm (Fig. 2), clearly

Table 4
Significant coefficients in polynomial regression models to determine diameter distribution shape in the treatments stands (CC=Clear cut; STC=Seed-tree cut; ISC=Irregular shelterwood cut; SC= selection cut; CON=Control).

	Coefficient			
Treatment	dbh	dbh2	dbh3	Distribution shape
CC	-3,3979***	0,6156	0,4663	NE
STC	-3,6901***	2,4205***	-0,5124	CO
ISC	-3,9082***	1,3288***	-0,8360*	RS
SC	-3,2854***	0,5609**	0,1617	CO
CON	-3,65821***	0,55313*	0,08671	CO

Regression model classifications are as follows: NE: negative exponential; RS: rotated sigmoid; CO: concave; according to Janowiak et al. (2008). * indicates p-values significance levels (‘***’= 0.001; ‘**’=0.01; ‘*’=0.05).

showed a separation according to shade tolerances in the NMDS1 axis, with the shade-tolerant species in the upper half and the shade-intolerant species in the lower half. The shade-intolerant species included mostly shrub and small tree species like *A. integrifolia*, *A. lanceolata*, *R. magallanicum* and *A. chilensis*, plus some pioneer tree species such as *W. trichosperma*, *E. cordifolia* and *D. diacanthoides*. The shade-tolerant tree species included the Podocarpaceae *P. nubigenus* and *S. conspicua*, the Mirtaceae *M. parviflora, M. ovata, L. apiculata,* and *A. meli. Laureliopsis philippiana*, one of the most shade-tolerant tree species in these forests, is also part of this group. Shade-intolerant species were associated with the silvicultural methods with the highest disturbance severity (CC and STC), whereas shade-tolerant species were associated with the selection cuts and the control plots. Several species appeared in an intermediate position in the NMDS1 axis, including some that behave as pioneer species like the two Proteaceae species *G. avellana* and *L. ferruginea*, *D. winteri,* and *C. paniculata*, and some considered more shade-tolerant species, such as *A. punctatum*, and the Mirtaceae *A. luma* and *M. planipes*. Several of these species were linked to the irregular shelterwood cuts, but most noticeably, *D. winteri* was associated to the seed-tree cuts. *D. diacanthoides* was selected as an indicator species in CC and STC based on Indicator Species Analysis, whereas *E. cordifolia* was an indicator for CC, *L. ferruginea* for ISC, and both *L. philippiana* and *S. conspicua* for SC and OG.

3.3. *Tree density among functional groups*

On average the functional group with the greatest tree density was midtolerant species (Fig. 3a). For this group the STC had the highest tree density, which did not significantly differ from the CC and ISC but differed from the SC and CON (with these four treatments not having significant differences between them). Short-lived shade-intolerant species were more abundant in the ISC, which did not significantly differ from the CC and STC but differed from the SC and CON, the latter being the only treatment that differed from all other treatments, having the lowest tree density for this functional group. There were no significant differences in tree density among treatments for long-lived shade-intolerant species (with very low densities) and shade-tolerant species (in the canopy or the understory).

For basal area (Fig. 3b) there were significant differences among treatments only for short-lived shade-intolerant, canopy shade-tolerant species and long-lived shade-intolerant species. Short-lived shade-intolerant species had more basal area in the ISC, and did not significantly differ from CC and STC but did differ from the SC and CON. Basal area of canopy shade-tolerant species was significantly lower in the even-aged methods compared to the other methods; this group had the highest basal area in SC, which did not significantly differ from CON and differed from the ISC. Volume (Fig. 3c) had significant differences among treatments for all species' groups except for midtolerant species, which had a very similar volume in all treatments. Long-lived shade-intolerant species had significantly higher volumes in CON than in the other treatments. Short-lived shade-intolerant species had more volume in the even- and two aged methods, which did not significantly differ among them, but the ISC significantly differed from SC and CON. Canopy shade-tolerant species had very low volumes in the even-aged methods, which significantly differed with SC and CON (ISC ranked intermediate for these species). Volume for understory shade-tolerant was significantly different only between CON (highest) and CC (lowest).

3.4. *Diameter distributions*

The diameter distribution was classified as Concave for STC, SC and CON, while it was a Negative Exponential for CC and had a Rotated-Sigmoid shape for ISC (Table 4 and Fig. 4). The diameter distributions for CC, STC and ISC were strongly influenced by the density and frequency of midtolerant species across diameter classes, and secondly by short-lived shade-intolerant species, but especially the absence (CC) or abundance (ISC) of large-sized trees determined their different shapes (Fig. 4). The SC and CON did not have long-lived shade-intolerant species, had a high tree density in mid- and large-sized trees, and a dominance of canopy shade-tolerant species throughout the distribution (Fig. 4). Also, the SC and CON showed abundant tree density of midtolerant tree species up to the 15–20 cm diameter classes, suggesting that these species are unable to survive under the heavy shade of canopy trees after they reach juvenile-adult ages.

3.5. *Tree heights*

All three even-aged methods developed a similar pattern of tree heights for dominant trees for the different functional groups (Fig. 5). While shade-intolerant species (both long- and short-lived) were the tallest in all even-aged cuts, trees in the short-lived shade-intolerant and both shade-tolerant groups were significantly taller in the ISC than in the CC and STC.

3.6. *Diameter growth*

Diameter growth showed important and significant differences in the even-aged methods compared to the SC and OG (Fig. 6). For the shade-intolerant species (Fig. 6a) there was a steady increase in diameter growth during the first decade after the even-aged cuts, a plateau in growth during the second decade, and a decline in growth afterwards. For each five-year period there were no significant differences in growth among the even-aged methods, although in general the ISC tended to have lower growth rates. For the midtolerant species (Fig. 6b) there were similar trends, but the decline during the last decade was shallower, and growth rates were significantly lower in the ISC compared to CC and STC after the first decade. Shade-tolerant species (Fig. 6c) had lower growth rates than the other functional groups following the even-aged methods, and differences among treatments were less pronounced, although even these shade-tolerant species maintained relatively higher growth rates in the CC. For all functional groups growth rates remained mostly unaltered during the entire period in SC and OG.

Diameter growth between shade-tolerance groups was compared for each treatment and in the control plots for the last 40 years (Table 5), which represented the mean annual increment for CC, STC and ISC and the mean increment of the last 40 years for SC and CON. We did not collect increment cores for shade-tolerant species in CC and STC since these species were uncommon in these treatments. Likewise, in the CON shade-intolerant species were nearly absent, so we did not collect increment cores for those species. Overall, diameter growth measurements were only available for all shade-tolerance groups in ISC and SC (Table 5). In CC, STC and ISC there were no significant differences in MAI between shade-intolerant and midtolerant species, but in the latter shade-tolerant species had a significantly lower MAI than the other tolerance groups. In SC and CON, growth over the last 40 years was significantly greater for midtolerant species compared to shade-tolerant

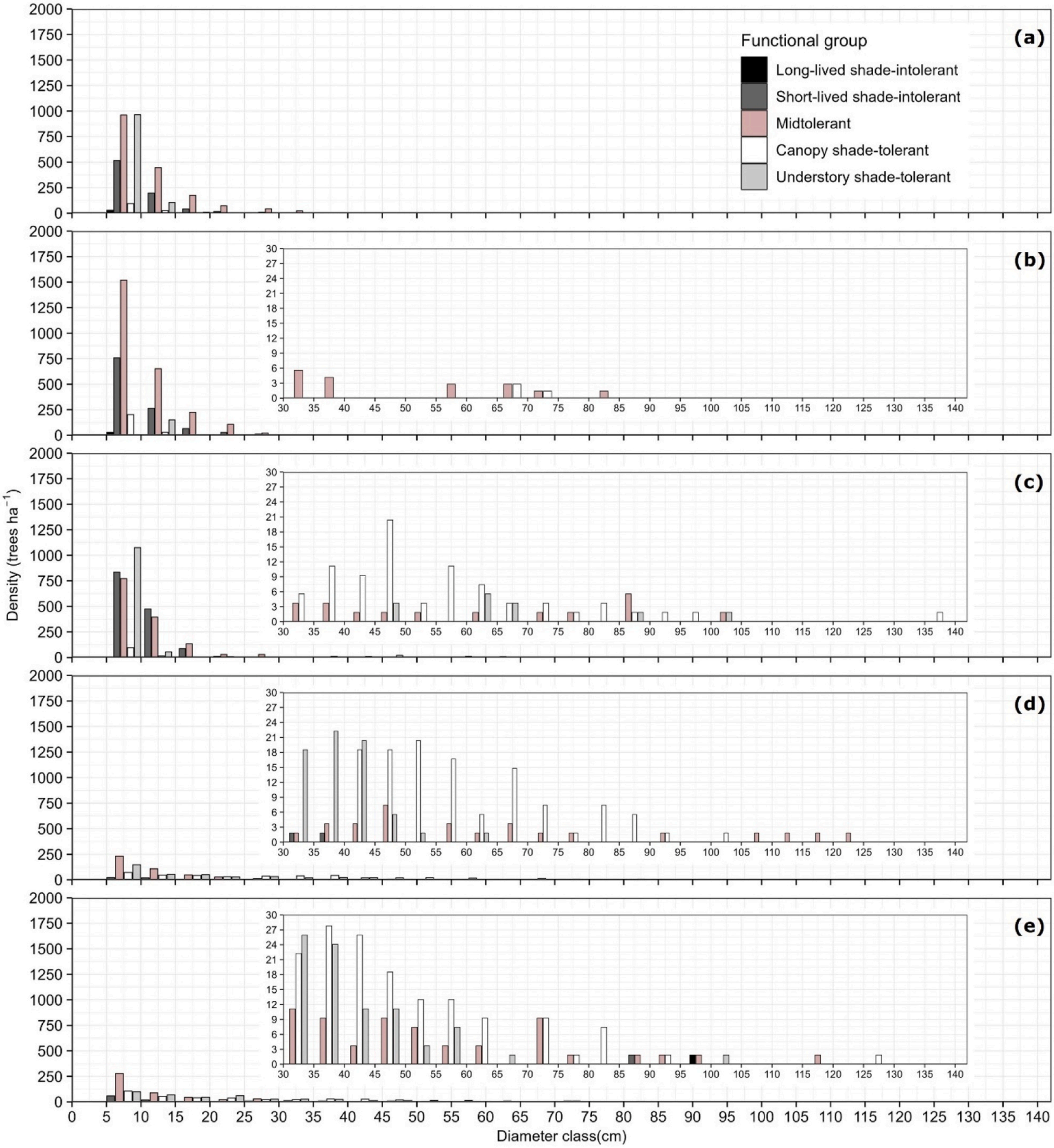

Fig. 4. Diameter distributions for the main tree species in a) Clearcut; b) Seed-tree cut, c) Irregular shelterwood cut, d) Selection cut, e) Control.

species.

3.7. Tree regeneration and cover of competing species

Tree regeneration was more abundant in the smaller size class (5–50 cm; Fig. 7a) and had low and similar numbers for the taller seedling classes (50–100 (Fig. 7b) and 100–200 cm (Fig. 7c)) and sapling classes (Fig. 7d). Density did not differ among treatments and with the control (CON) forest for any seedling class, although shade-tolerant species nearly doubled their density in the SC and CON compared to that in the even-aged cuts (Fig. 7a). For the sapling class there were no trees in the SC and the CON for shade-intolerant species, and for shade-tolerant species the STC and ISC cuts had significantly greater densities than the other treatments and the CON.

The cover and importance of the bamboo *Chusquea machrostachya* and the fern *Lophosoria quadripinnata* are presented in Table 6. *Chusquea* had high cover (25–41%) in CC, SC and OG, and low cover (4–7%) in the STC and ISC cuts. *Lophosoria quadripinnata* had a similar cover (7–12%) in all treatments and was lowest (2.2%) in the control OG forest.

4. Discussion

4.1. Overall differences among silvicultural methods

For this work, we sought to evaluate and compare results from different silvicultural methods representing a range of harvest severities

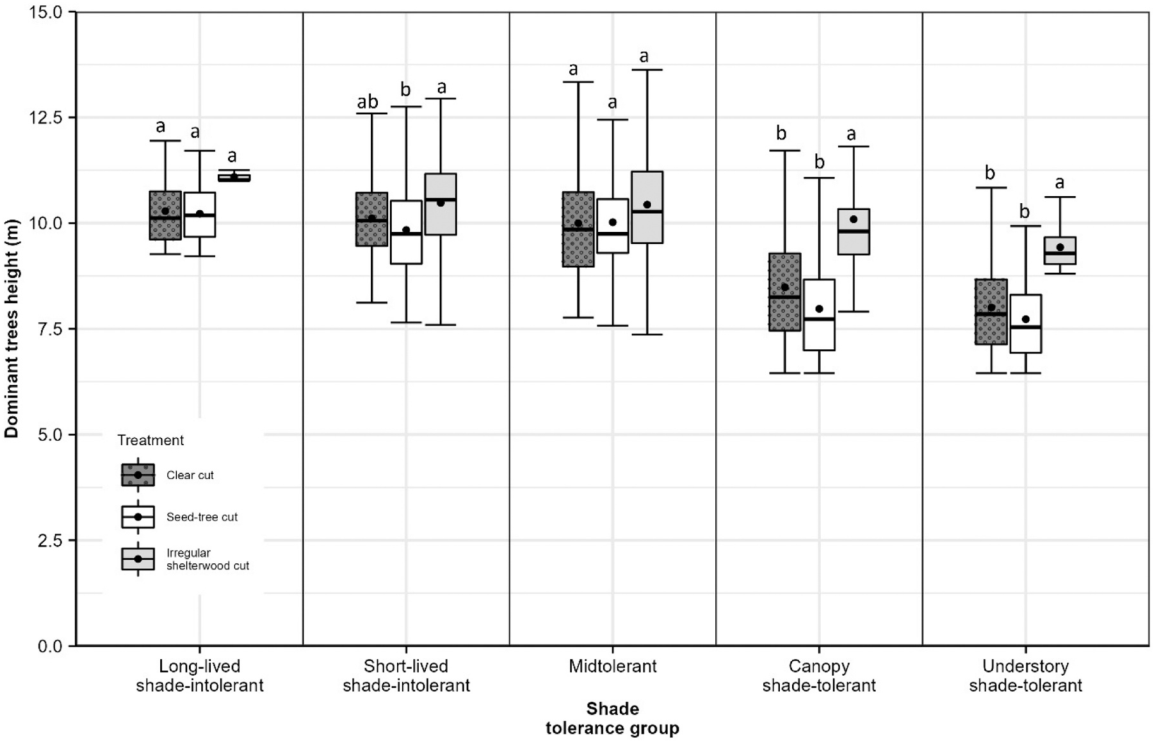

Fig. 5. Dominant height by functional groups for the even-aged cuts. Different letters within each panel for each functional group indicate significant differences.

after almost four decades since implementation, through the assessment of tree growth, regeneration, composition and structure. The study included two even-aged silvicultural methods (clear cut and tree-seed cut), one two-aged method (irregular shelterwood cut in its extended alternative; *sensu* Raymond et al. 2009) and one slightly implemented uneven-aged method (selection cut) that only corresponded to the initial cut and was not followed by periodic cuts based on a cutting cycle as usually occurs with the selection system (*sensu* Nyland, 2016). These were compared to the old-growth forests of the study area, which served as the control treatment. Differences in structure and composition reflected the level of disturbance severity associated with a given method, with the greatest differences occurring between the high severity (i.e., clearcut (CC)) and the CON plots. The low severity selection cut resulted in similar values to the CON, whereas the higher severity seed-tree (STC) treatment tended to be closer in its values to the CC, although it had greater values for tree density, basal area and volume. In general, the irregular shelterwood plots (ISC) ranked intermediate, and had the least variability in structural variables among all treatments (Table 2). The ISC, did not have significant differences in tree densities with CC and STC for any functional group, but was dominated by two short-lived shade-intolerant species(*L. ferruginea* and *G. avellana*), whereas the even-aged cuts were dominated by midtolerant species. Nevertheless, the ISC had a relatively high tree density of the midtolerant *E. cordifolia*, probably the species with highest timber value in these forests. Tree density and basal area/volume, as well as saplings (considered established regeneration) were higher in ISC and STC than in CC (significantly in the latter case). In contrast, in a similar experiment but in the Andes , at age 26 after the cuts Donoso et al. (2019) reported significantly greater values in tree density and basal area in the case of clearcuts, with a major dominance in tree density of *E. coccineum* (short-lived shade-intolerant) followed by midtolerant species. In this latter case, the greater tree densities in the clearcuts relative to those in the present study could be the result of a combination of two things: a) better tree seedling growth vs. *Chusquea* competition in the more productive site in the Andes, and b) greater mortality of *Chusquea quila,* a shade-intolerant species (*C. machrostachya* in the Coast is shade tolerant) in the Andes once tall saplings or juvenile trees created enough shade to kill it.

At the regeneration level, the two even-aged methods and the two-aged method resulted in similar numbers of seedlings, but the density of saplings (usually considered established regeneration) was significantly greater in STC and ISC compared to CC, a result that is likely explained by the much lower cover of the competing *C. machrostachya* bamboo (e.g., see Donoso and Nyland, 2005) in the understory of the STC and ISC cuts. Also, an interesting result was that trees of all five functional groups were taller in the ISC compared to STC and CC (a significant difference in three groups), suggesting that the partial canopy cover of the residual trees in ISC had a positive effect on height growth of these trees. While this behavior is common in midtolerant tree species (Wagner er at. 2011), it is not commonly reported for shade-intolerant species, but is presumably due to an initial advantage for these species in the present study due to lower understory competition in areas with some canopy cover. In contrast, diameter growth was lower in the ISC than the CC and STC for all shade tolerance groups, a pattern consistent with other work examining sapling growth across a range of canopy openness (Lin et al. 2002). Similar trends were also observed in comparisons between clear cuts with shelterwood cuts in New York hardwood forests after 26 years, in which midtolerant tree species were more abundant in shelterwoods, but growth rates were higher in the clearcuts (Nyland et al. 2000).

In addition to the above comparisons, the old-growthness (*sensu* Bauhus et al. 2009) of the forest conditions resulting from each of the silvicultural methods evaluated can be estimated through the old-growth index (OGI) developed by Ponce et al. (2019). This OGI includes total tree density, three expressions of basal area (total, of trees > 80 cm and of shade-tolerant species) and the GINI coefficient, and was developed for the Evergreen forest type in medium- to good-quality sites. Using the OGI formula, the SC and the OG have an OGI of 66 and 64%, the CC and the STC an OGI of 7 and 6%, and the ISC an OGI of 41%. Thus, the ISC, by maintaining large-tree legacies through the residual trees left after the cut, can retain many old-growth attributes, while also allowing the development of a new cohort, like what occurred with CC and STC.

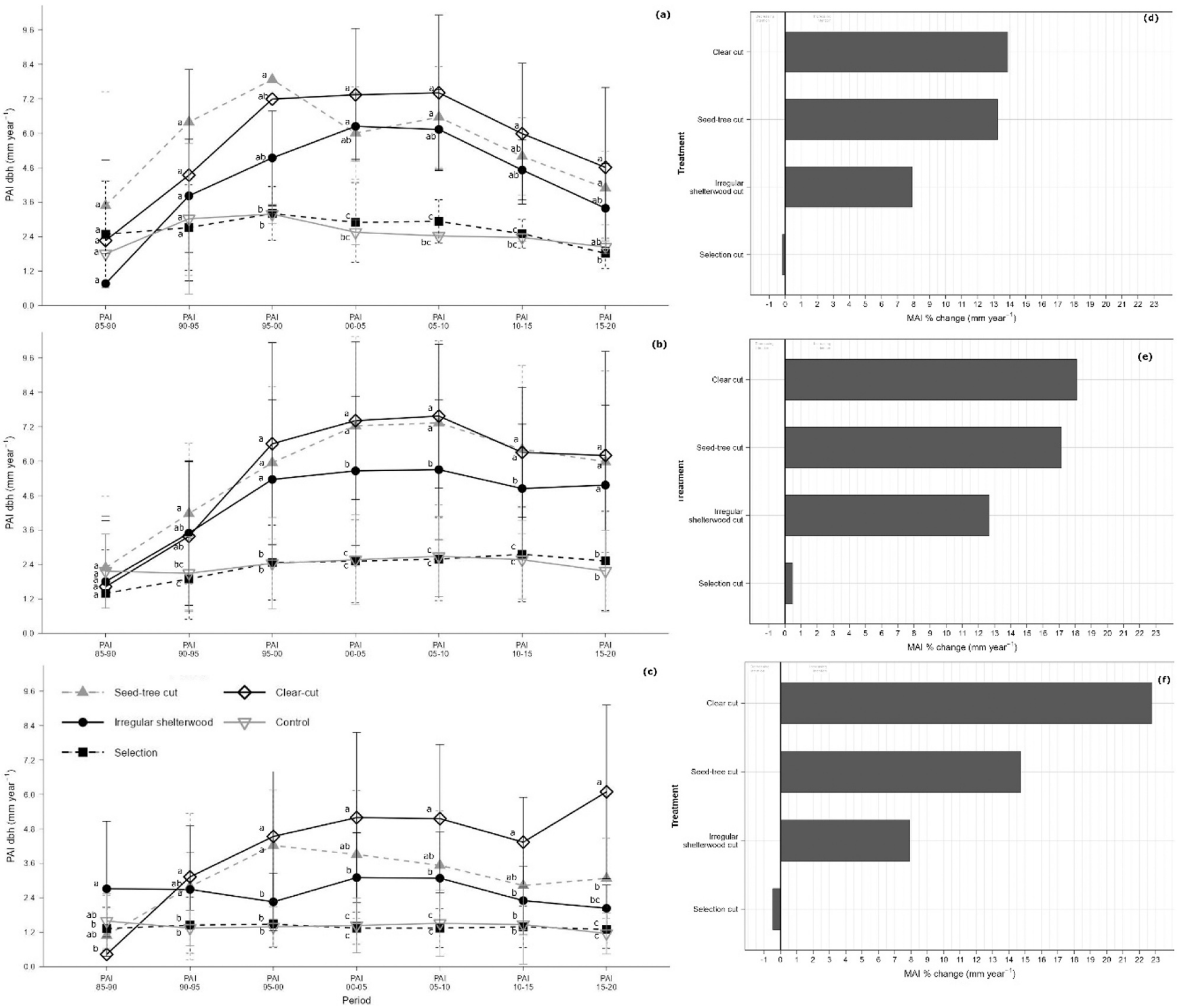

Fig. 6. Periodic annual increment (PAI) in diameter between treatments for a) shade-intolerant species; b) mid-tolerant species and c) shade-tolerant species. X-axis labels correspond to five-year periods, starting in year 1985 (after the cuttings). Different letters indicate significant differences between PAI for each treatment (p < 0,05). Figures in the right column represent the percentage change of the Mean Annual Increment (MAI) with respect to the control situation after 40 years of applying the cuts for d) shade-intolerant species; e) mid-tolerant species and f) shade-tolerant species.

Table 5
Diameter increment (and standard deviation; mm) for tree species according to shade-tolerance groups and treatment for the last 40 years, which corresponds to mean annual increment in CC, STC and ISC. Values with the same letter did not differ between tolerance groups. CC: Clear cut; STC: Seed-tree cut; ISC: Irregular shelterwood cut; SC: Selection cut; CON: Control.

Shade tolerance	CC		STC		ISC		SC		CON	
Intolerant	7	8.0±1.6 a	13	6.7±1.3 a	11	5.1±1.0 a	7	3.0±0.8 a	0	-
Midtolerant	61	6.7±2.0 a	46	6.4±2.4 a	61	5.4±1.9 a	17	2.9±0.9 a	13	3.1±1.1 a
Shade-tolerant	0	-	0	-	10	2.5±0.2 b	30	1.4±0.6 b	25	1.3±0.6 b
Total cores	68		59		82		54		38	

Overall, even- and two-aged cuts have a rapid development, but in the case of the poor-quality site of this study, intermediate-severity disturbances (especially ISC) seem to yield the best results in terms of jointly maintaining a high tree richness, a rich vertical structure, and developing economically valuable new cohorts for landowners looking for timber production. We do not discard the prospects for uneven-aged silviculture as an economically and ecologically viable option for these sites, as in other Evergreen forests (Schnabel et al. 2017, Donoso et al. 2020), but from the current study we cannot recommend them. It is likely that selection harvest that included tending of the immature diameter classes, may have generated more ecologically and economically desirable results (Nyland, 2016); however, the low level of harvesting across diameter classes in the selection cuts we examined precluded such outcomes. Actually, selection cuts with low residual

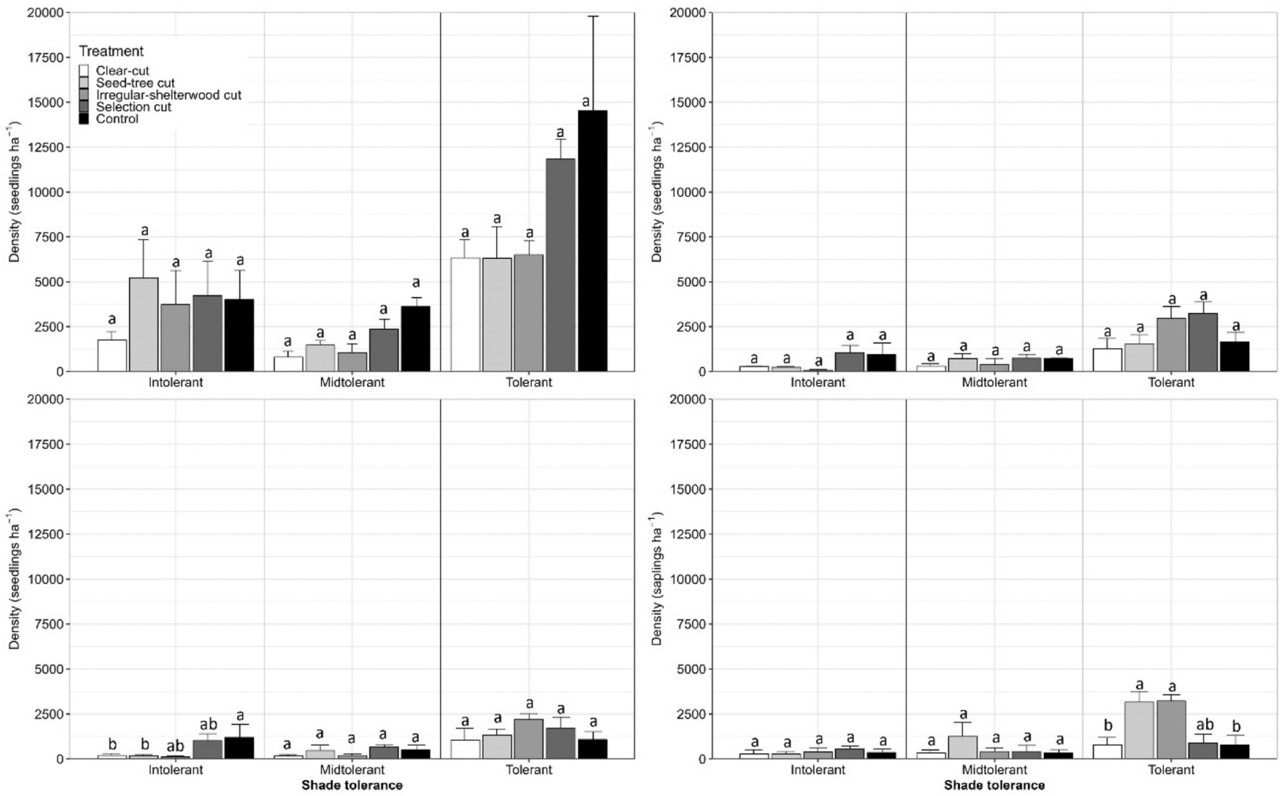

Fig. 7. Tree regeneration in each silvicultural method by functional groups and height ranges for seedling: a) 5–50 cm; b) 50–100 cm; c) 100–200 cm and d) saplings (<5 cm DBH and >200 cm height). Different letters indicate statistically significant differences between functional groups ($p < 0.05$).

Table 6
Cover (C (%)) and importance value (IV) of the two main competing species after four decades of response to different silvicultural methods in the coastal evergreen forest type. C represents plant cover (%) and IV the importance value for the species. CC: Clear cut; STC: Seed-tree cut; ISC: Irregular shelterwood cut; SC: Selection cut; CON: Control.

	CC		STC		ISC		SC		CON	
Species	C (%)	IV	C (%)	IV	C (%)	IV	C (%)	IV	C (%)	IV
Chusquea macrostachya	28,75	29,52	4,68	11,4	6,73	10,76	40,67	32,58	24,6	35,55
Lophosoria quadripinnata	7,08	8,76	11,23	23,27	11,67	19,37	9,68	9,82	2,18	6,98

basal areas have proved to yield better growth rates (Donoso et al. 2020) and long-term incomes (Draper et al. 2021), while maintaining a high biodiversity but losing some structural complexity (Schnabel et al. 2017). One major problem in the forests at the sites of this study is the high cover of the bamboo *C. macrostachya*, which is shade tolerant and exerts a strong competition on tree species regeneration (Donoso and Nyland, 2005). Results in this study suggest that only the STC and the ISC, with their partial residual canopy cover, were able to limit the development of this bamboo species.

4.2. *Implications for management*

Balancing conservation and timber production is a matter of increasing concern, especially where old-growth forests are an important component in the landscape (Donoso et al. 2014). Many proposals in this regard promote silvicultural practices that maintain a continuous cover (e.g., Puettmann et al. 2015, Pukkala and v. Gadow, 2012), and follow the development models of local native forests (Palik et al., 2021). Several authors (Palik and D'Amato, 2024, Palik et al., 2021, D'Amato et al., 2011) have proposed that the two main silvicultural methods that may better allow the maintenance or development of natural forests' structural and compositional attributes across different successional stages are the selection system and the irregular shelterwood cuts. Also, different studies (Niese and Strong, 1992, Draper et al. 2021) have been consistent in suggesting moderate- or intense-severity single-tree selection cuts to provide the best long-term economic yields. As mentioned above, in our study, the selection method did not yield significant differences in growth and regeneration compared to the old-growth forest. The ISC cut did provide results that balance the development of a diverse and dense new cohort, with good growth rates in tree species of high timber value, while also maintaining many old-growth attributes. These types of cuts seem promising at these sites and in the Andes ((Donoso et al., 2019)) but require more studies that include a wider range of residual densities and partial removals of residual trees after some time to release the new cohorts developed after the initial cut. Similarly, although less successful in sustaining old-growth attributes, the STC presents an ecologically beneficial alternative to CC through retention of some large tree-legacies while also recruiting a diverse mix of species. Similar benefits have been observed in retention harvests with similar low levels of dispersed retention to those used in STC in this study (Urgenson et al. 2013). Consideration of harvest season is also important for future work, since maximum seed production and dissemination is different for the diversity of tree species in the Evergreen forest type (Donoso 1989b). These studies in addition should cover the diversity of forest sites and species that can be encountered across the area (3,5 million ha; CONAF,

2021) covered by the Evergreen Forest Type (e.g., Donoso and Navarro, 2022, Bannister and Donoso, 2013, Gutiérrez et al. 2009).

Across the even-aged methods examined, the lowering diameter growth rates observed during the third decade after implementation suggest that these systems may benefit from the applications of thinning during this time period. This thinning should focus mostly on a significant reduction of the short-lived shade-intolerant species, most of which belong to the Proteaceae family and jointly (*G. avellana*, *L. ferruginea*, *E. coccineum*) have a 18–30% importance value. This would be particularly critical for ISC, which is the treatment with the highest proportion with these species. A similar proposal is given by Donoso et al. (2019) for secondary forests developed after the implementation of even- and two-aged silvicultural methods in Andean Evergreen forests, with a massive regeneration of *E. coccineum*. While these Proteaceae species will naturally and gradually fade away, their high density and rapid initial growth rates create significant competition for valuable timber species. Their timely thinning may also render valuable wood for small-sized timber and furniture. In addition, Navarro et al. (2011) estimated that thinning of *D. winteri* secondary forests at age 30 would yield trees of 29 cm in dbh (a merchantable diameter for sawlogs) at age 51, compared to trees 16 cm in dbh at the same age without thinning. Reducing the tree density and basal area of the residual trees in even- and two-aged methodsmay also provide incomes to the landowner and allow a more rapid recruitment of the new cohort. Overall, these silvicultural treatments may allow an enrichment of the vertical structure of the forest and could also increase the biomass of dead wood in the system (downed and standing, the latter through girdling), which is considered a valuable structural element in managed forest ecosystems (Palik et al., 2021).

Long-term evaluations of silvicultural experiments are essential to provide forest managers and owners with strong information to support their decisions regarding which silvicultural systems may best meet long-term ecological and economic objectives. Given the great uncertainty surrounding future climate and disturbance regimes, forest managers should aim for forests with high structural complexity and species diversity, which provide multiple pathways to adapt to future disturbances. At the same time, these managed forests should also be economically valuable to provide incomes to the landowners, so recruitment of desirable species and promotion of rapid tree development is also critical. Overall, the two-layered ISC cuts better represent a general balance between these various ecological and economic attributes after four decades of development, including structurally diverse, compositionally rich and fully stocked forest conditions where the new cohort is becoming dominated by commercially valuable tree species. To this end, mid-severity cuttings (e.g., an intermediate-severity disturbance) in this forest type would make a greater contribution than high- or low-severity cuttings to climate-smart forestry (cf. Bowditcha et al. 2020, Verkerka et al. 2020), i.e., would deliver complex and productive forests while also providing timber that retains carbon and replaces fossil-intensive materials, especially in the construction industry

CRediT authorship contribution statement

Pablo Jorge Donoso: Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Tomás Riquelme-Buitano:** Methodology, Data curation. **Celso Omar Navarro:** Writing – review & editing, Methodology, Investigation. **Daniel Patricio Soto:** Writing – review & editing, Methodology, Investigation. **Anthony W. D′Amato:** Writing – review & editing, Methodology, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Data Availability

Data will be made available on request.

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