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Shelterwood cut intensity determines recovery pathways of managed *Nothofagus pumilio* forests †

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Abstract

Background: Forest harvesting is the main driver of change in forest structure and natural regeneration dynamics during management. Forest recovery after disturbances is important for economic values and ecological processes of natural forests. The aim of the study was to assess recovery paths of *Nothofagus pumilio* (Poepp. & Endl.) Krasser forests regarding stand structure, environmental characteristics and regeneration values after two harvest intensities of shelterwood regeneration cuts during four different periods after harvesting (YAH).

Methods: A total of 59 stands harvested under shelterwood regeneration cuts, including four YAH periods (0-2, 3-10, 11-40, >40 years), and 41 unmanaged stands of *N. pumilio* forests were sampled in Tierra del Fuego, Argentina. Forest structure, environmental characteristics and regeneration values were measured and compared by analyses of variance, using harvesting intensity, YAH and age structure as main factors. These variables were used to calculate different indices to define recovery pathways for the different treatments.

Results: Forest structural variables such as basal area and total volume over bark differed between harvesting intensities, and the differences with unmanaged forests tend to decrease over time. Soil variables did not significantly differ among young and mature unmanaged forests or managed forests under low or high harvesting intensities. In contrast, light availability presented differences in unmanaged forests compared to managed forests among different harvesting intensities and YAH, although the gap decreased with time particularly beyond 40 YAH. Some regeneration variables, such as seedling density, differed among young and mature unmanaged forests, but did not change with harvesting intensity. Other regeneration variables, such as seedling height and sapling density increased with YAH. The forest index (FI), environment index (EI), and regeneration index (RI) showed different pathways for harvested forests over time, where greater changes were observed for high intensity shelterwood cuts. The differences, compared to unmanaged forests, drastically reduced beyond 40 YAH, regardless of harvesting intensity.

Conclusions: Forest structural, environmental and regeneration variables followed different pathways over time for the studied harvesting intensities of shelterwood regeneration cuts when compared to unmanaged forests. As expected, greatest differences on all these variables from natural conditions occurred when more intense harvesting was carried out. Our results suggests that *N. pumilio* forests were resilient to shelterwood regeneration cuts regarding forest structure, regeneration, and environmental conditions (soil properties and light availability), reaching comparable values to unmanaged forests beyond 40 YAH.

Keywords: Harvest intensity; environmental characteristics; regeneration; resilience; recovery; natural forest; unmanaged forest; Southern beech

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Introduction

There is an increasing global pressure to preserve ecosystems to sustain biodiversity and the benefits of nature to humanity (Díaz et al. 2019). Ecological knowledge of native forests, as ecosystem services providers, is the base to guide conservation and production strategies (Thuiller 2007). Many ecosystem services are mechanistically linked to specific forest structural attributes and therefore their recovery is bounded to regeneration and resilience (Sutherland et al. 2016). Nevertheless, site related conditions can drastically change following human interventions, and can lead to natural regeneration failure, e.g., by making unfavourable seedbed conditions, insufficient light at the understorey level, or by releasing competing understorey vegetation, resulting in undesirable structures at the stand scale (Dey et al. 2019). Hence, a key process for sustainable forestry is ensuring successful natural regeneration (Dey 2014).

Silvicultural practices and harvesting intensity can limit the recruitment of original tree species (Martínez Pastur et al. 2021). Similarly to the natural dynamic process, harvesting creates gaps of various sizes (Promis 2018) depending on cut intensity, which influences the recruitment and growth of natural regeneration (Dobrowolska 2006; Paredes et al. 2020). After harvesting, the species assemblage of understorey plants undergoes changes as the crown cover evolves (Pérez Flores et al. 2019), potentially competing with natural regeneration (Toro Manríquez et al. 2019). Moreover, intense harvesting can have a negative impact on soil properties, such as soil carbon loss, reduced nutrient contents, and soil acidification resulting from altered microbial activity, influenced by changes in soil physical properties (Achat et al. 2015a; Achat et al. 2015b). Under these conditions, tree growth may slow down, tree mortality may increase as a result of logging damage, and greater vulnerability to disturbances affecting ecosystem functioning may occur (Achat et al. 2015a; Picchio et al. 2020).

The resilience of harvested forests depends primarily on the success of natural regeneration, which is essential for ensuring long-term spatial continuity of the forest canopy. Naturally regenerating forests exhibits key properties such as heterogeneity, self-organization and adaptation, which makes them complex adaptive systems with the capacity for recovery or persistence after natural and human disturbances (Chazdon & Guariguata 2016). For example, *Nothofagus* regeneration in mixed forests after applying the regeneration cut in the shelterwood method failed to achieve pre-harvest species assemblage, influenced by variations in microsite and stand conditions (Sola et al. 2020). Natural *Nothofagus pumilio* (Poepp. & Endl.) Krasser (commonly named lenga) forests in Tierra del Fuego are mainly regenerated under gap dynamics, either produced by tree uprooting or by windthrow, that creates gaps of different sizes (Rebertus & Veblen 1993; Promis 2018). The widely applied shelterwood cut system seeks to recreate this natural dynamic (Martínez Pastur et al. 2000), and the natural regeneration response to logging is sought in the context of conservation and ecological sustainability (Dezzotti et al. 2003). As a result of intensive harvesting, a homogeneous forest structure is obtained, providing numerous management advantages (e.g., even-aged and fully stocked stands, where silviculture can be easily applied due to its homogeneity) (Martínez Pastur et al. 2000). Immediately after harvesting, forest structure deteriorates although recovery has been observed 20 years after harvesting (YAH) (Martínez Pastur et al. 2017), yet long-term paths remain understudied. Second-growth forests comprise a high proportion of the global forest area, and therefore it becomes important to track long-term recovery trajectories of the managed forests and their ecosystem services (Sutherland et al. 2016).

Various silvicultural proposals have been implemented in *N. pumilio* forests of Tierra del Fuego, e.g. clear-cuts, selective cuts, shelterwood cuts, and variable retention, which primarily differ in harvest intensity, economic performance and conservation targets (Martínez Pastur et al. 2009; Amoroso et al. 2021; Donoso et al. 2022). The shelterwood system aims to remove original overstorey in successive cuttings leaving remanent protective trees to promote natural regeneration (Schmidt et al. 2003; Donoso et al. 2022). The first, preparation cut can be applied for the renewal of the stand, by increasing the diameter of the stems, removing undesirable seed-source or low-quality individuals and expanding the tree crowns that will produce the seeds (Prévost & Gauthier 2013; Donoso et al. 2022). The system scheme is followed by a regeneration or disseminatory cut, which is intended to open the site for regeneration to be established under the protection of parent trees (Schmidt et al. 2003, Peri et al. 2021; Donoso et al. 2022). When regeneration occupies most of the harvested area and is well established, remaining old trees are removed in a final cut, and the secondary even-aged structure is managed through thinning and pruning (Martínez Pastur et al. 2009). Although shelterwood system was prescribed in early 1990 in Tierra del Fuego, an incomplete management has been applied, as preparatory cuts are not traditionally applied and the final removal of larger, older trees following regeneration cuts has been neglected (Gea-Izquierdo et al. 2004). In addition, harvest intensity across the landscape is variable, mainly explained by processing technology, harvesting machinery and terrain, that in turns affects the remanent forest structure and regeneration quality (Paredes et al. 2020). Given the widespread application of the shelterwood system and its potential impact on conservation values (Martínez Pastur et al. 2009; Martínez Pastur et al. 2002a), it becomes important to understand the recovery patterns of forests harvested under different management intensities compared to unmanaged forests growing under natural dynamics.

On the other hand, unmanaged forests under natural dynamics can have dissimilar age structure. A natural cycle based on age structure has been described for other *Nothofagus* forests (Martínez Pastur et al. 2021). Based on Schmidt & Urzúa (1982), forest age structure is described by four developmental phases: optimal initial growth (< 40 years old), optimal final growth (40-120 years old), mature (120-220 years old) and decay (> 220 years old), all identifiable by the bark appearance. There are commonly two or more of these phases coexisting within the same stand. Distinguishing among these phases is crucial, as they determine forest structure (Martínez Pastur et al. 2002a; Martínez Pastur et al. 2021), which in turn, influence microhabitat availability for biodiversity (Baker et al. 2020), functional complexity (Bauhus et al. 2009) and carbon stock (Aravena Acuña et al. 2023), among others. Therefore, understanding the natural variation of age structure in unmanaged forests becomes crucial for better comprehending recovery paths of secondary forests.

The concept of ecological resilience is central for assessing forest recovery after disturbances such as harvesting (Briske et al. 2006; Puettmann et al. 2013; Bryant et al. 2019). However, resilience is difficult to quantify due to multiple factors that contribute or affect their magnitude and recovery pathways (Bryant et al. 2019). Here we consider resilience as ecological stability, particularly measured as the time length to recover the pre-disturbance state (Orians 1975; Donohue et al. 2013). Thus, the aim of the study was to evaluate forest resilience under shelterwood cuts (after regeneration cuttings), considering different harvesting intensities and times after intervention (0 to > 40 YAH), compared to unmanaged natural forests. We focused our analysis in three dimensions: forest structure, environmental characteristics (soil properties and light availability) and regeneration values. We hypothesised that the recovery of forest structure and original stand conditions depends on harvesting intensity and YAH. Our predictions are that: (i) forest structure differs among unmanaged forests and among harvest intensities and time elapsed after cuttings; (ii) environmental characteristics are similar within unmanaged forests but differ in harvested forests (iii) regeneration success is dependent on harvesting intensity; and (iv) recovery of forest structure and stand conditions is dependent on harvesting intensity and time elapsed after harvesting.

Methods

Study site

We selected a total of 100 homogeneous stands, ranging from 1 to 18 ha, comprising unmanaged (n = 41) and managed stands (n = 59) of *N. pumilio* forests in Tierra del Fuego, Argentina (Figure 1). We classified the unmanaged stands in young (YUF, n = 11, <100 years-old) and mature forests (MUF, n = 30, 100-350 years-old) based on the proportion of basal area (BA) corresponding to the different development phases according to Schmidt & Urzúa (1982). Thus, when 70 % of the total basal area of the stand was dominated by the young development phases, we classified it as YUF, and otherwise as MUF. Uneven-aged stands with more than two dominant phases reaching over 70% of area basal were not chosen for this study. Managed stands under the shelterwood system after the regeneration cut (SC) were classified according to YAH: (i) SC1 = 0-2 YAH, (ii) SC2 = 3-10 YAH, (iii) SC3 = 11-40 YAH, and (iv) SC4 = > 40 YAH. Each group was split in two categories of harvesting intensity: low (L) and high (H), based on BA removal (40-80% and > 80% of BA removal) (Figure 2). Total number of sampled stands for each category were: SC1-L = 4, SC1-H = 6, SC2-L = 4, SC2-H = 8, SC3-L = 6, SC3-H = 7, SC4-L = 16, and SC4-H = 8 stands.

Sampling design

In each stand, we randomly placed a 50 m length transect for the measurements. At the beginning and end of the transect, we measured two forest inventory plots using the point sampling method (BAF= 1-5) with a Criterion RD-1000 (Laser Technology, USA), measuring for each tree: (i) diameter at breast height (DBH) with a forest calliper, (ii) development phase (young or mature) (based on Schmidt & Urzúa 1982), and (iii) vigour (VIG) (1-3, where higher values indicated more vitality). We also measured (iv) dominant height (DH) of the stands, using a TruPulse 200 (Laser Technology, USA) by averaging the two taller trees per stand (at a maximum distance of 50 m). Based on these data we determined site quality (SQ), tree density (DEN), basal area (BA), total over bark volume (TOBV), quadratic mean diameter (QMD), and mean total volume annual growth (GRO) following Martínez Pastur et al. (2002b). The GRO variable is the expected volume increment per year according to models of *N. pumilio* for the region, based on site quality (obtained from DH), and development phase of each independent tree (Martínez Pastur et al. 2002b). The calculated values are then averaged for the entire stand and displayed as growth per ha per year.

We also characterized the stands with hemispherical photographs taken at the same places of forest inventory plots with a fisheye 8 mm lens (Sigma, Japan) mounted on a 35 mm digital camera (Nikon, Japan) and orientating the upper edge towards the magnetic north. Using these photographs and the Gap Light Analyzer v.2.0 software (Frazer et al. 2001), we estimated crown cover (CC) as a percentage of open sky relative to the cover, relative leaf area index (RLAI) as the effective amount of leaf surface area per unit ground area integrated over the zenith angles 0-60°, and total solar radiation at understorey level (TR) as the amount of direct (DRR) and diffuse solar radiation (DFR) transmitted through canopy as a percentage of radiation incident on a horizontal surface located above the forest canopy. Parameters and details for these calculations are available in Martínez Pastur et al. (2011).

We also collected four soil samples (0-10 cm depth) per plot with a soil corer of known volume. We weighted the samples before and after oven-drying to obtain soil bulk density (SD) and soil water content (WC) averaged from the four samples. For chemical analysis, we sieved the pooled samples to remove elements > 2 mm using a 2 mm sieve. We determined: (i) total soil organic carbon (C) from soil samples washed with HCl (50%) by an automatic analyser (LECO CR12, USA), (ii) total nitrogen (N) by a semi-micro Kjeldahl method, and (iii) extractable phosphorus (P) according to Bray & Kurtz (1945).

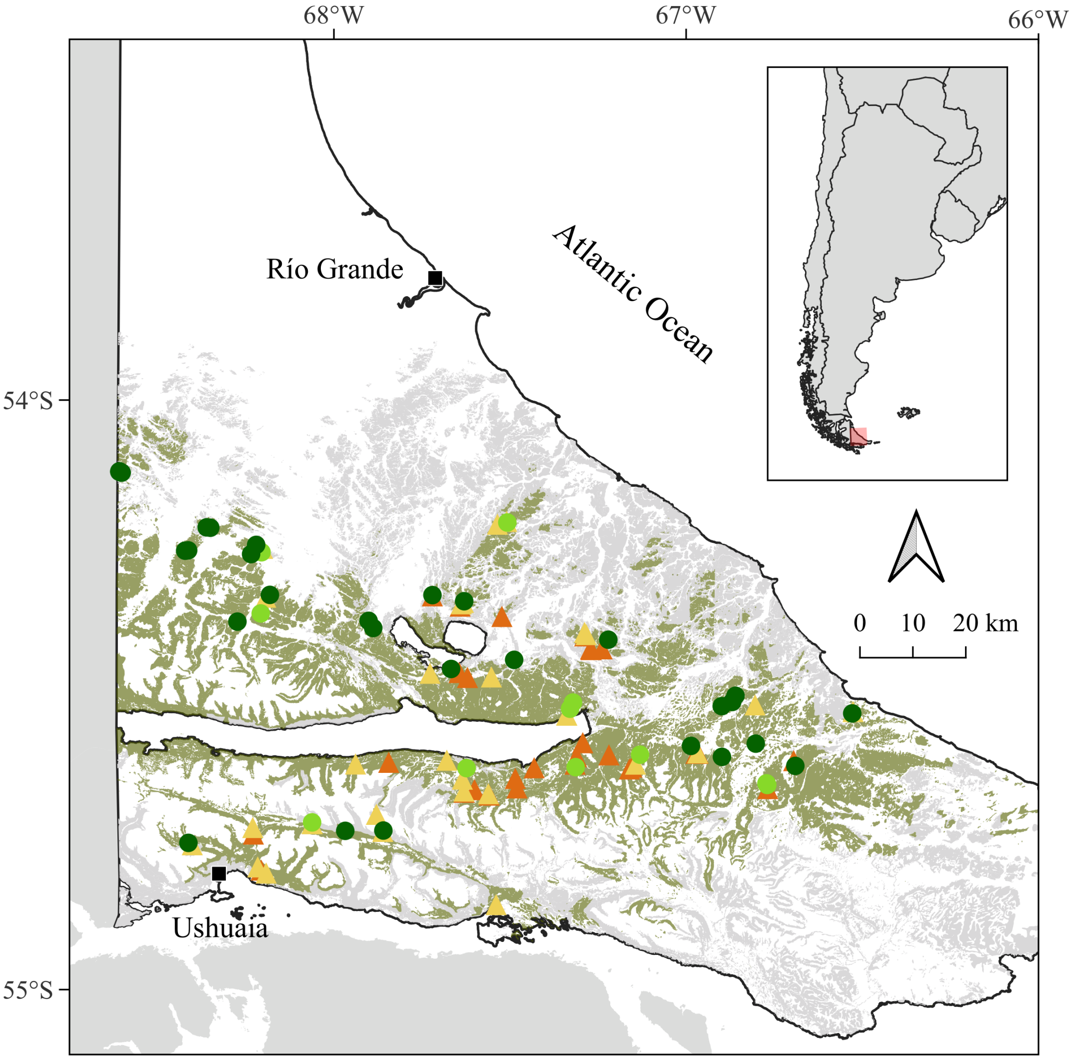

FIGURE 1: Sampled stands of *Nothofagus pumilio*: mature (dark green dots) and young unmanaged stands (light green dots), low (yellow triangles) and high (orange triangles) intensity shelterwood regeneration cuts. Green area shows pure *N. pumilio* forests in Tierra del Fuego, Argentina.

Finally, we measured regeneration classified as seedlings (SE, < 1.3 m height) and saplings (SP, ≥ 1.3 m height, < 5.0 cm DBH) in 1 m^2 plots and 5 m^2 plots, respectively, at both the beginning and the end of each transect. We calculated total density (DEN-SE, DEN-SP), mean height (H-SE, H-SP) and plant quality (Q-SE, Q-SP) as the percentage of regeneration free of damage and good stem shape.

Statistical analysis

We compared the sampled unmanaged stands considering the age structure (YUF and MUF) as main factor for one-way analyses of variance (ANOVA), and managed stands regarding harvesting intensity and YAH as main factors for two-way ANOVAs. When a two-way ANOVA was unfeasible due to unbalanced design, we use one-way ANOVA to test each factor separately. After the ANOVAs, we tested significant differences among levels with a Tukey test ($p < 0.05$) regarding: (i) forest structure characteristics (BA, CC, RLAI, DH, VIG, DEN, TOBV, QMD, GRO), (ii) environmental stand characteristics (DRR, DFR, TR, SD, WC, C, N, P), and (iii) forest regeneration values (DEN-SE, H-SE, Q-SE, REC, DEN-SP, H-SP, Q-SP). We assessed three indices to evaluate recovery pathways following Martínez Pastur et al. (2021): forest index (FI), environment index (EI), and regeneration index (RI) using the above-mentioned variables. Thus, we standardised each variable (0-1) using the minimum and maximum observed value for all plots. Then, we averaged each set of variables to obtain the indices. We represented with zero the absence of one variable value (e.g. seedling height when no seedlings were found) in the index construction. We also calculated the standard error of each index for further graph comparisons.

FIGURE 2: Examples of sampled stands including unmanaged (MUF: mature, YUF: young) and managed forests under low or high intensity shelterwood regeneration cuts (SC-L or SC-H) across different times elapsed after harvesting (YAH): SC1: 0-2 YAH, SC2: 3-10 YAH, SC3: 11-40 YAH, and SC4: > 40 YAH.

Results

When analysing the forest structure of unmanaged forests, YUF stands presented more BA, DEN and GRO, and less DH, TOBV and QMD compared to MUF stands (Table 1, Table A1). In the managed stands, SC-L had greater BA, CC, RLAI, TOBV, and QMD compared to SC-H. When comparing YAH periods, BA, CC, RLAI, DEN, and TOBV increased over time, while DH showed lower values after the 3-10 YAH period while QMD decreased over time. Few interactions were found such as the one for DEN due to a marked change between periods SC3 and SC4 for SC-H, exceeding SC-L only at the end of the evaluated periods. A significant interaction was also observed for CC that slowly increased during the first studied periods for SC-H compared to SC-L to reach similar values 40 YAH.

DRR and TR were greater for YUF compared to MUF, with no differences detected in other environmental variables (Table 2). When managed stands were analysed, SC-H presented greater solar radiation at understorey level than SC-L, but no differences were found for the measured soil variables. Solar radiation-related variables (DRR, DFR and TR) significantly decreased with time (YAH) tending towards values typical of unmanaged forests. Soil variables did not change with time after harvesting (YAH).

When forest regeneration variables were analysed, MUF presented greater DEN-SE than YUF, but the other related variables did not differ between unmanaged stands (Table 3). Besides, only four MUF stands presented saplings (unlike YUF that had none) with an average height of 1.95 m mostly (62.5%) exhibiting good sapling quality. There were no significant differences in forest regeneration variables between harvesting intensities. When analysing YAH, an increase in H-SE and DEN-SP during the third period followed by a decrease after 40 YAH was observed. Seedling (Q-SE) and sapling quality (Q-SP) did not differ among YAH or harvest intensities (Table 3).

Forest structure and environmental indices showed similar trends between young and mature unmanaged stands, although large differences were detected in the forest regeneration values (Figure 3). In general terms, low intensity harvesting (SC-L) had similar values in the three analysed indices to unmanaged forests compared to high intensity harvesting (SC-H) during the first periods (<40 YAH). However, a greater variation was observed in SC-H (Fig. 3). Moreover, in SC-L, the environmental conditions (EI) were greatly modified at SC1-L, although during the following periods they tend to recover to the original unmanaged forest values. In SC-H, the greater modifications of environmental (EI) and forest structure

TABLE 1: Analyses of the variance (ANOVA) for forest structure characteristics: (i) one-way ANOVAs considering young (YUF) and mature (MUF) unmanaged forests, and (ii) two-way ANOVAs considering shelterwood regeneration cut (SC) intensities (SC-L: low, SC-H: high), and years-after-harvesting (YAH) as main factors. BA = basal area (m^2 ha^{-1}), CC = crown cover (%), RLAI = relative leaf area index, DH = dominant height (m), VIG = vigour (1-3), DEN = tree density (trees ha^{-1}), TOBV = total over bark volume (m^3 ha^{-1}), QMD = quadratic mean diameter (cm), GRO = annual volume tree growth (m^3 ha^{-1} yr^{-1}).

ANOVA	Treatment	Level	Parameter								
			BA	CC	RLAI	DH	VIG	DEN	TOBV	QMD	GRO
(i)	Unmanaged forests	YUF	68.6b	85.4	2.08	18.9a	2.48	3022b	501.3a	28.8a	7.6b
		MUF	60.1a	87.7	2.27	21.8b	2.47	431a	591.0b	57.5b	3.9a
		F	8.26	2.16	1.60	6.15	<0.01	26.78	4.79	90.56	22.82
		p	0.007	0.150	0.213	0.018	0.952	<0.001	0.035	<0.001	<0.001
(ii)	A: Intensity	SC-L	34.4b	73.6b	1.48b	20.6	2.23	785	279.7b	58.0b	2.7
		SC-H	20.3a	62.6a	1.08a	20.9	2.06	1241.79	159.3a	50.3a	2.0
		F	18.28	13.63	6.94	0.21	1.96	0.76	11.08	4.77	1.68
		p	<0.001	0.005	0.011	0.652	0.168	0.387	0.002	0.034	0.201
	B: YAH	SC1	19.8a	58.5a	0.77a	22.8b	2.03a	101a	171.0a	67.2c	1.5a
		SC2	24.8a	62.0a	0.96a	20.0a	2.10ab	200a	189.8a	56.1bc	1.7a
		SC3	21.2a	64.9a	1.22a	20.2ab	1.99a	811a	164.1a	52.4ab	1.6a
		SC4	43.7b	87.0b	2.18b	20.1a	2.47b	2941b	352.9b	41.0a	4.5b
		F	15.43	25.39	22.11	2.81	4.61	8.48	8.58	10.79	10.69
		p	<0.001	<0.001	<0.001	0.049	0.006	<0.001	<0.001	<0.001	<0.001
	A x B	F	0.36	2.80	1.18	0.59	0.92	3.17	0.19	0.87	1.20
		p	0.780	0.049	0.326	0.624	0.440	0.032	0.904	0.460	0.319

F = Fisher test, p = probability. Different letters indicate significant differences by the Tukey test at p <0.05.

TABLE 2: Analyses of variance (ANOVA) of environmental and soil variables: (i) one-way ANOVAs considering young (YUF) and mature (MUF) unmanaged forests, and (ii) two-way ANOVAs considering shelterwood regeneration cut (SC) intensities (SC-L: low, SC-H: high), and years-after-harvesting (YAH) as main factors. DRR: direct solar radiation (%), DFR: diffuse solar radiation (%), TR: total solar radiation (%), SD: soil bulk density (g cm^{-3}), WC: soil water content (%), C: total soil carbon (%), N: total soil nitrogen (%), P: total soil extractable phosphorus (ppm).

ANOVA	**Treatment**	**Level**	**Parameter**							
			DRR	**DFR**	**TR**	**SD**	**WC**	**C**	**N**	**P**
(i)	Unmanaged forests	YUF	20.3b	19.4	19.5b	0.74	42.3	10.9	0.405	51.8
		MUF	15.7a	16.0	15.8a	0.78	56.2	12.0	0.422	59.8
		F	5.49	3.49	4.39	0.25	0.73	0.23	0.07	0.36
		p	0.024	0.069	0.043	0.619	0.397	0.637	0.800	0.554
(ii)	A: Intensity	SC-L	36.2a	34.3a	34.6a	0.79	47.8	10.2	0.370	49.1
		SC-H	49.2b	48.1b	48.1b	0.75	58.9	10.4	0.372	44.2
		F	9.41	15.65	14.45	0.53	1.50	0.02	<0.01	0.38
		p	0.003	<0.001	<0.001	0.468	0.226	0.894	0.978	0.542
	B: YAH	SC1	55.9b	53.8b	54.1b	0.85	62.3	10.6	0.371	54.4
		SC2	52.9b	48.9b	49.5b	0.78	54.7	9.7	0.350	41.9
		SC3	43.4b	44.7b	44.3b	0.76	50.4	9.8	0.373	37.2
		SC4	18.7a	17.3a	17.5a	0.70	45.9	11.2	0.390	53.1
		F	20.68	29.40	28.03	1.24	0.63	0.30	0.13	1.22
		p	<0.001	<0.001	<0.001	0.304	0.597	0.828	0.941	0.311
	A x B	F	1.27	3.10	2.66	0.44	1.03	1.14	2.05	0.69
		p	0.295	0.035	0.058	0.728	0.385	0.342	0.119	0.558

F = Fisher test, p = probability. Different letters indicate significant differences by the Tukey test at p <0.05.

(FI) occurred at SC2-H. However, regeneration did not greatly change during the first two periods (SC1-L and SC2-L), while SC3-L presented the greatest divergence compared to MUF. Subsequently, recovery occurred >40 YAH. Under high harvest intensity, forest regeneration values change during the earlier periods (e.g., SC2-H) compared with the low harvest intensity, reaching its maximum dissimilitude during the third period (SC3-H). Finally, shelterwood regeneration cuts >40 YAH were similar to unmanaged stands for all indices, regardless of harvesting intensity.

Discussion

Forest structure of *Nothofagus pumilio* has been studied across different natural gradients, e.g. site quality, rainfall regimes, altitude and temperature (Martínez Pastur et al. 2000; Massaccesi et al. 2008; Brand et al. 2022; Soto et al. 2022). Our study showed that several structural differences can also be associated to age structure of young and mature unmanaged stands. Our results showed that for relatively comparable basal areas, contrastingly different tree density and QMD, major differences are detected in volume for the analysed age structures. This is related not only with occupancy degrees, but also with site quality and dominant height (Martínez Pastur et al. 1997). Trees in young stands are in competition, occupying all the available growing space, and rapidly respond to minor disturbances, preventing new individuals to establish (Oliver & Larson 1996). As tree grows, trees with competitive advantages differentiate in diameter and height, and when trees become larger and older, they occupy the growing space less aggressively, allowing for regeneration to establish (Oliver & Larson 1996). Thus, the decrease in stand density is buffered by remaining trees by responding to availability of resources, increasing growth and compensating for the removals in mature stands (Pretzsch 2009). This forest dynamics can explain the high density of trees with small DBH, small basal area and total volume found in YUF, and the opposite pattern in MUF. These differences were also reported for other *Nothofagus* forests growing undisturbed (Armesto et al. 1992; Burrascano et al. 2013; Martínez Pastur et al. 2021).

Our prediction about environmental conditions of the unmanaged forests was partially true, because young and mature forests were similar regarding soil properties, but differ in light availability, which can influence regeneration values. Forest stand age and structure have been reported to influence soil variables in managed stands of Mediterranean forests (Lucas-Borja et al. 2016). Similarly, differences in soil nutrients and soil moisture can affect overstory growth in mixed forests (Lévesque et al. 2015; Oktavia et al. 2022). Mature forest trees have shown an influence on soil properties

TABLE 3: Analyses of variance (ANOVA) for forest regeneration variables: (i) one-way ANOVAs considering young (YUF) and mature (MUF) unmanaged forests, and (ii) two-way ANOVAs considering shelterwood regeneration cut (SC) intensities (SC-L: low, SC-H: high), and years-after-harvesting (YAH) as main factors. DEN-SE = seedling density (thousand ha^{-1}), H-SE = seedling height (cm), Q-SE = seedling quality (%), REC = recruitment (thousand ha^{-1}), DEN-SP = sapling density (thousand ha^{-1}), H-SP = sapling height (cm), Q-SP = sapling quality (%).

ANOVA	Treatment	Level	Parameter						
			DEN-SE	**H-SE**	**Q-SE**	**REC**	**DEN-SP**	H-SP§	**Q-SP§**
(i)	Unmanaged forests	YUF	182.3a	5.4	92.1	20.5	0.0	-	-
		MUF	584.3b	10.4	93.4	121.7	0.2	2.0	62.5
		F	5.08	1.15	0.04	1.27	0.98	-	-
		p	0.030	0.292	0.851	0.266	0.328	-	-
(ii)	A: Intensity	SC-L	178.0	26.3	93.7	47.3	4.5	4.01	73.3
		SC-H	67.6	37.0	96.0	1.3	5.5	3.36	75.9
		F	2.24	1.43	0.14	2.14	0.23	0.50	0.05
		p	0.141	0.239	0.711	0.149	0.633	0.484	0.826
	B: YAH	SC1	74.6	32.8ab	95.3	0.4	1.3a	1.8a	47.7
		SC2	278.8	30.5ab	97.5	64.7	2.1a	2.3a	90.9
		SC3	61.4	57.7b	88.7	0.0	12.0b	2.4a	83.1
		SC4	76.4	5.8a	97.9	32.0	4.7ab	5.9b	70.3
		F	1.82	5.62	0.69	0.86	5.62	10.24	1.64
		p	0.155	0.003	0.563	0.466	0.002	<0.001	0.203
	AxB	F	0.84	2.74	0.34	0.84	1.72	-	-
		p	0.477	0.055	0.798	0.481	0.174	-	-

F = Fisher test, p = probability. Different letters indicate significant differences by the Tukey test at p <0.05.

§ One-way analysis of variance performed for unbalanced design.

in boreal forest (Kuuluvainen 2002). However, we found no relationship between unmanaged forest age structure and soil properties, as they exhibited similar values. This pattern also occurred in *N. antarctica* forests in Tierra del Fuego (Martínez Pastur et al. 2021), indicating that these characteristics are not influenced along the natural development stages cycle described by Schmidt and Urzúa (1982). In addition, forest regeneration can be affected by several factors, such as canopy closure, woody debris and understorey cover, as was evidenced in harvested stands and in different unmanaged forests (Caldentey et al. 2009; Martínez Pastur et al. 2007, 2011). Here, forest regeneration was favoured in mature forests compared to young ones, and this cannot be solely explained by canopy cover or light availability, as was pointed out in other studies (Caldentey et al. 2009). In this sense, probably microsite and resource availability (e.g. soil moisture) are leading this pattern, partly explained by a lower basal area and tree density (Paredes et al. 2020). It can also be explained by higher seed production observed in mature unmanaged forests compared to young forests, where most of the trees have not reached the reproductive stage (Martínez Pastur et al. 2008; Rodríguez-Souilla et al. 2023a).

Forest structure changes are more notorious during the first periods following the regeneration cut and under high intensity harvesting, but tend to recover to similar values to unmanaged forests over time, in accordance with our predictions. As expected, forest structure was influenced by harvest intensity, particularly basal area, crown cover, RLAI, total volume and QMD, but no change in height, tree density or growth was detected. Variations in forest structure features based on different cutting intensities have been documented in both Amazonian and temperate forests (Parrotta et al. 2002; Martínez Pastur et al. 2021). Moreover, most forest structure features reached similar values to mature unmanaged forests with time, such as crown cover, relative leaf area index, vigour and tree growth. However, others variables were more closely associated with young unmanaged forests in the studied periods, e.g., basal area, total over bark volume, and tree density. This indicates that forest structure was well recovered around 40 YAH, where most of the studied variables were significantly different from previous periods being more similar to unmanaged forests. Studies in temperate rainforests have also shown that young secondary forests (40-100 YAH) develop structural characteristics, like basal area or total volume, similar to old-growth forests in a relatively short time period (LePage & Banner 2014, Sutherland et al. 2016). This early structural recovery is associated with wood volume, coarse woody debris, and carbon storage (Sutherland et al. 2016; Chaves et al. 2023).

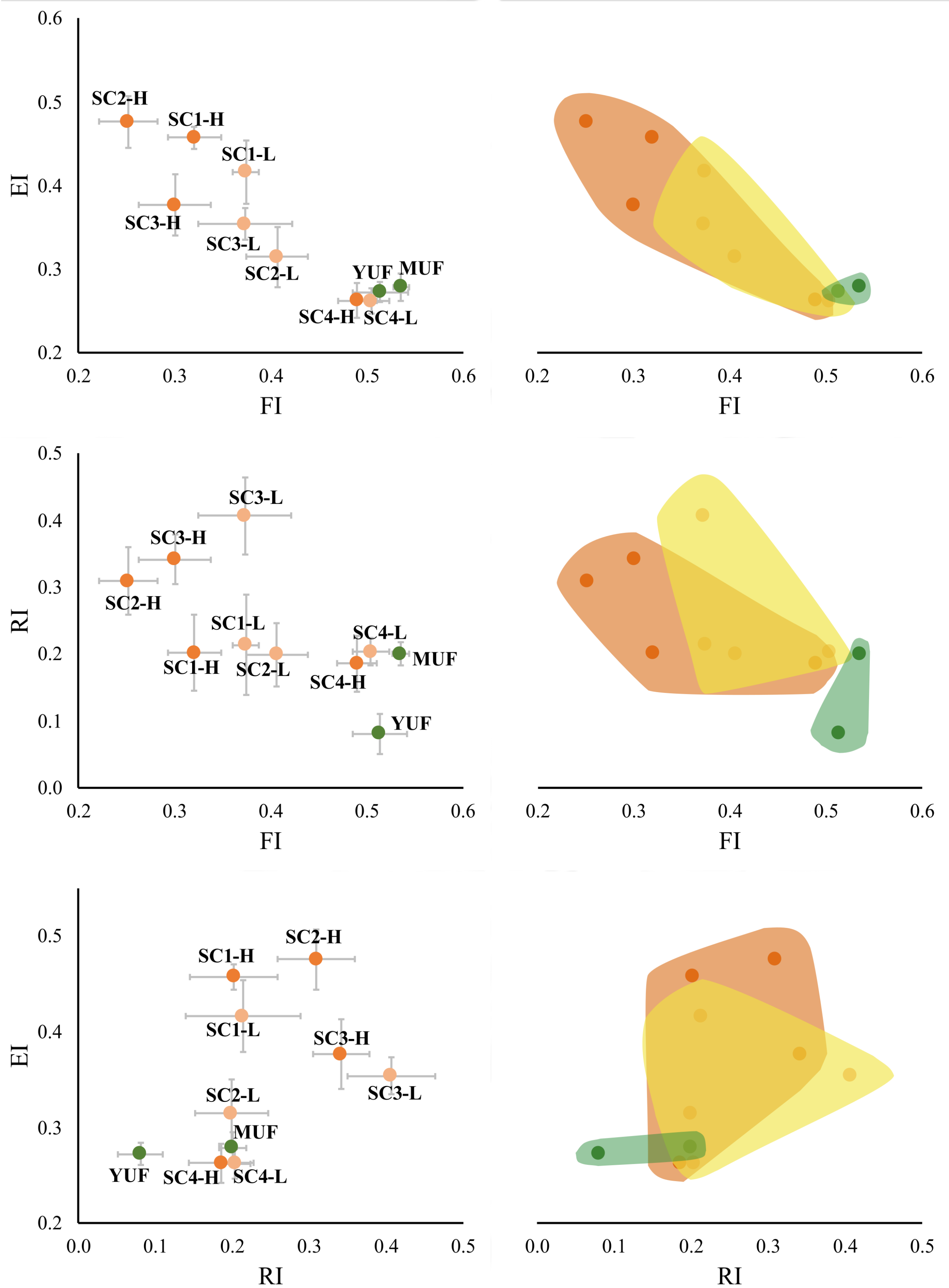

FIGURE 3: Relationships among grouped set of variables for unmanaged (YUF: young, MUF: mature) and managed (SC-L: low, SC-H: high intensity shelterwood regeneration cut, across years elapsed after harvesting SC1: 0-2, SC2: 3-10, SC3: 11-40, SC4: >40) stands of *Nothofagus pumilio*. Left side shows average values and standard error for different indices (FI = forest structure, EI = environmental characteristics, RI = forest regeneration values). Right side shows the total variation area for unmanaged stands (green), high (orange) and low (yellow) intensity shelterwood regeneration cuts.

Like unmanaged forests, managed forests only partially change environmental characteristics, as soil properties remain unchanged, but shifts occurred in light availability over time and with harvest intensities. Solar radiation at understorey level is closely related to crown cover, and varied with YAH tending to the values observed on closed forests, reaching minimum values particularly at > 40 YAH. Light availability and the effective rainfall at understorey level are limiting factors for forest regeneration (Caldentey et al. 2005; Martínez Pastur et al. 2007), being favoured by intermediate crown cover levels and its associated radiation level (Martínez Pastur et al. 2011). The harvesting intensity can also influence forest floor or mineral soil nutrient stocks by different factors (Hume et al. 2018). In our case, despite a slight decrease in C, N and P concentrations in managed versus unmanaged forests, no effect of intensity or time on soil features was detected among the studied stands. Probably, both harvesting intensities create similar micro-site conditions by leaving most of the litter, small branches and bark on site, and thus reducing the negative impacts on soil fertility (Achat et al. 2015a). In the stands with more intense harvesting, e.g., whole tree removal, where there is a lack of litterfall input and a noticeable increase in light and soil temperatures, a negative effect in soil is observed (Hume et al. 2018). Small-size gaps (< 200 m^2) as a silvicultural treatment have shown faster recovery of the physical, chemical and biological soil properties compared to more intensive harvesting treatments as clear-cuts (Jourgholami et al. 2021). Our study showed that shelterwood regeneration cuts, regardless of their intensity and YAH, are successful in maintaining soil stability and highlight their resistance to perturbation at stand level in the analysed conditions.

Harvest intensity had no impact in regeneration success although some changes are observed over time after the intervention. Increased light availability has been identified as the major predictor of *N. pumilio* regeneration (Heinemann et al. 2000; Ivancich et al. 2011; Promis 2018). Nevertheless, regeneration values are closely linked not only to forest structure and light and resource availability, but also to seed supply and pre- and post-harvest seedlings establishment (Cuevas 2002; Martínez Pastur et al. 2008, 2011; Rodríguez-Souilla et al. 2023b). The lack of a significant effect of harvest intensity on regeneration could be explained by a great variability and heterogeneity of stands conditions (Caldentey et al. 2009). Low intensity cuts, however, exhibited a tendency to higher density of initial regeneration and recruitment, which could suggest that a favourable balance exists between the crown cover of the overstorey (e.g. shelter and seed source) and the available resources (e.g. light and water availability) (Martínez Pastur et al. 2007, 2011). This pattern may extend to other low-intensity harvesting methods, such as selective cuts, known for their multiple benefits for biodiversity conservation and ecosystem services provision (Atlegrim & Sjöberg 2004). Nevertheless, it is essential to consider a cost-gain balance (Nordén et al. 2019; Peri et al. 2022). In any case, seedlings and saplings densities for all treatments were among the adequate values cited in the literature for different unmanaged and managed *Nothofagus* forests (Martínez Pastur et al. 1999; Chauchard et al. 2008; Collado et al. 2008; Paredes et al. 2020; Sola et al. 2020).

The proposed indices showed that young and mature unmanaged forests tend to be more similar compared with harvested stands. This is consistent with other studies that showed the similarity of forests growing under natural dynamics (Martínez Pastur et al. 2021). The most significant finding of this research was the existence of different recovery pathways according to harvesting intensity, in line with our predictions. High intensity harvesting showed the greatest modification in forest structure, environmental characteristics and regeneration values compared to low intensity across the YAH. Nonetheless, after 40 YAH both, high and low shelterwood regeneration cut intensities, were similar and with unmanaged forests. However, these findings should be interpreted with caution: the similarity in the forest structure index for both treatments is due to compensation of variables, e.g., higher tree density with lower volume, diameter and basal area for high intensity and the opposite for low intensity. There are other aspects to take into account in the managed forest ecosystem such as biodiversity, e.g., higher tree density with small diameters and low basal area may modify bird species assemblage (Benitez et al. 2022). Thus, as we hypothesised, this study showed that forest regenerates under the intensities analysed, and that the ecosystem response after shelterwood regeneration cuts tend to recover initial values depending on harvest intensity and time after the intervention. Therefore, this study supports the idea that shelterwood regeneration cuts, in the analysed intensities, maintain *N. pumilio* forest resilience in Tierra del Fuego.

Conclusions

Shelterwood regeneration cuts in *N. pumilio* forests have shown evidence of adequate regeneration, independently of harvest intensity and years after harvesting. Forest structure, environmental characteristics and regeneration followed different recovery pathways over time and with harvesting intensity, undergoing major modifications from natural conditions, particularly when high intensity management is applied in contrast to lower intensities. *N. pumilio* forests seem resilient under different shelterwood regeneration cut intensities regarding their capacity to maintain adequate regeneration levels and stable environmental conditions, reaching comparable values to unmanaged forests in relatively short periods of time.

List of abbreviations

ANOVA: analysis of variance
BA: basal area
C: total organic carbon
CC: crown cover
DBH: diameter at breast height

DEN: tree density
DEN-SE: total density of seedlings
DEN-SP: total density of saplings
DFR: diffuse solar radiation
DH: dominant height
DRR: direct solar radiation
EI: environmental index
FI: forestall index
GRO: mean total volume annual growth
H-SE: mean height of seedlings
H-SP: mean height of saplings
MUF: mature unmanaged forests
N: total nitrogen
P: total phosphorus
QMD: quadratic mean diameter
Q-SE: mean quality of seedlings
Q-SP: mean quality of saplings
RI: regeneration index
RLAI: relative leaf area index
SC: shelterwood regeneration cut
SC-H: high intensity shelterwood regeneration cut
SC-L: low intensity shelterwood regeneration cut
SD: soil bulk density
SE: seedlings
SP: saplings
SQ: site quality
TOBV: total over bark volume
TR: total solar radiation at understorey level
VIG: vigour
WC: soil water content
YAH: years after harvesting
YUF: young unmanaged forests

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

Conceptualisation: JEC, JMC, PLP and GMP; methodology: JMC, MVL and GMP; data collection: JEC, JR-S, JMC and GMP; formal analysis: JEC and GMP; project administration: PLP, and GMP; writing original draft: JEC and GMP. All authors read and approved the final manuscript.

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Appendix

Table A1: Mean and standard deviation of forest structure variables for young (YUF) and mature (MUF) unmanaged forests, and harvested forests under low or high intensity shelterwood cuts (SC-L or SC-H) through the four studied time periods of years after harvesting (YAH): SC1: 0-2 YAH, SC2: 3-10 YAH, SC3: 11-40 YAH, and SC4: >40 YAH. BA = basal area (m^2 ha^{-1}), CC = crown cover (%), RLAI = relative leaf area index, DH = dominant height (m), VIG = vigour (1-3), DEN = tree density (trees ha^{-1}), TOBV = total over bark volume (m^3 ha^{-1}), QMD = quadratic mean diameter (cm), GRO = tree volume growth (m^3 ha^{-1} yr^{-1}).

Level	BA	CC	RLAI	DH	VIG	DEN	TOBV	QMD	GRO
YUF	68.6 (± 11.4)	85.4 (± 5.2)	2.08 (± 0.36)	18.9 (± 4.0)	2.5 (± 0.4)	3022 (± 2794)	501.3 (± 82.6)	28.8 (± 10.7)	7.6 (± 3.9)
MUF	60.1 (± 7.2)	87.7 (± 4.0)	2.28 (± 0.47)	21.8 (± 3.1)	2.5 (± 0.3)	431 (± 149)	591.0 (± 126.0)	57.5 (± 7.7)	3.9 (± 1.0)
SC1-L	26.3 (± 7.7)	62.1 (± 8.2)	0.90 (± 0.29)	22.4 (± 1.8)	2.2 (± 0.3)	129 (± 128)	205.6 (± 36.7)	70.7 (± 13.6)	1.8 (± 0.5)
SC1-H	13.3 (± 2.2)	54.8 (± 6.5)	0.67 (± 0.20)	23.2 (± 2.6)	1.9 (± 0.4)	73 (± 29)	136.4 (± 42.4)	63.7 (± 14.5)	1.1 (± 0.4)
SC2-L	32.8 (± 5.3)	73.7 (± 8.0)	1.38 (± 0.43)	20.9 (± 2.0)	2.4 (± 0.3)	285 (± 77)	262.3 (± 69.8)	57.7 (± 7.0)	2.5 (± 0.7)
SC2-H	16.8 (± 7.7)	50.3 (± 13.5)	0.56 (± 0.33)	19.1 (± 2.1)	1.9 (± 0.5)	115 (± 61)	117.2 (± 53.1)	54.5 (± 9.1)	1.0 (± 0.6)
SC3-L	30.1 (± 8.4)	70.8 (± 12.8)	1.48 (± 1.14)	20.0 (± 1.7)	2.0 (± 0.5)	1171 (± 2238)	232.8 (± 82.4)	54.7 (± 9.7)	2.2 (± 1.3)
SC3-H	12.3 (± 5.4)	59.0 (± 20.7)	0.97 (± 0.70)	20.5 (± 2.6)	2.0 (± 0.6)	451 (± 865)	95.5 (± 34.2)	50.0 (± 19.0)	1.0 (± 0.6)
SC4-L	48.6 (± 17.3)	87.6 (± 3.2)	2.23 (± 0.34)	20.5 (± 3.5)	2.5 (± 0.3)	1555(± 1249)	418.0 (± 213.5)	48.9 (± 10.8)	4.1 (± 2.5)
SC4-H	38.8 (± 12.9)	86.4 (± 4.2)	2.18 (± 0.47)	19.7 (± 1.8)	2.4 (± 0.4)	4328 (± 4157)	287.9 (± 89.9)	33.1 (± 12.9)	4.9 (± 3.0)