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Article

Forest carbon management strategies influence storage compartmentalization in *Nothofagus antarctica* forest landscapes

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Abstract

Silvopastoral systems are one of the strategies proposed to manage natural forests in southern Patagonia for livestock and timber purposes. In the context of climate change, it is necessary to design new management proposals to improve forest carbon sequestration. The objective was to quantify the innate carbon stocking (t C ha^{-1}) variation in *Nothofagus antarctica* forests under natural dynamics in even- and uneven-aged structures, and in harvested and transformed stands. Carbon stocks were sampled in 145 forest stands, identifying 14 different components in above- and belowground strata. Results showed that the carbon content of the stands varied significantly with age (e.g., C contribution of different tree components), ranging from 289 to 386 t C ha^{-1}. Deadwood was the variable that varied most among the successional stages. In harvested stands, carbon content changed significantly with increasing harvesting intensity (from 84.6% to 55.7%) and was lower than in non-harvested stands. These changes were reflected in reduced carbon accumulation in trees, deadwood, and soil layer and increased accumulation in understory plants. Silvopastoral system management can achieve a balance between productive objectives and maintenance of carbon stocks in managed forests, resulting in higher resilience and lower carbon losses, thus promoting sustainable forest management.

Key words: carbon storage, forest carbon management, carbon accumulation, silvopastoral management, carbon content, above- and belowground

Introduction

Forests are the key components of the global carbon cycle, regulating atmospheric CO_2 concentrations (Kurz et al. 2013). Carbon stored in forest ecosystems is distributed both above- (e.g., trees and understory plants) and belowground (e.g., soil layer and root system, including coarse and fine roots) and can be found stored in tissues in various states of decomposition (e.g., litter, coarse woody debris (CWD)) or even dead (e.g., standing dead trees) (IPCC 2006; Bravo et al. 2017). Hence, the capacity of the forests to sequester and maintain carbon stored in wood and soil biomass in the medium-to-long term has been widely recognised (Ontl et al. 2020), as well as their potential to provide a multitude of goods (e.g., timber and fuelwood) and services (e.g., maintenance of biodiversity, recreational values, soil retention, scenic beauty, and regulation of the hydrological cycle) that are increasingly valued by society (Duncker et al. 2012). However, trade-offs between different uses (e.g., harvesting or conservation) have unusually been considered. The relationship between different forest ecosystem services (ES) can be synergistic, as has been demonstrated in the case of carbon and wood production through the transfer of carbon from forest to wood products (Ruddell et al. 2007; Duncker et al. 2012). Therefore, one of the most important questions for the future is how to manage ES, balancing their use, conservation, enhancement and maintenance. In this context, forest carbon management (FCM) has been proposed to increase or maintain the amount of carbon sequestered in managed stands (e.g., decreasing forest harvest intensity to decrease carbon losses to the atmosphere) (Birdsey et al. 2000).

Silvopastoral systems combine livestock production and timber harvesting on the same unit of land, highlighting that advantages offered by these systems include productive diversification, erosion control, and carbon sequestration (Peri et

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al. 2016*a*). This strategy has been widely applied to manage *Nothofagus antarctica* (G.Forst.) Oerst. forests at southern Patagonia (Peri et al. 2016*b*), aiming to conserve natural characteristics in managed stands and maintain long-term sustainability by ensuring stand preservation (Peri et al. 2022). The importance of knowing the carbon sequestration capacity of the *N. antarctica* forest ecosystem would reinforce the theory that silvopastoral systems is a silvicultural management strategy that contributes to the adaptation and mitigation of climate change-related problems (Oliva et al. 2017). This requires an accurate estimation of carbon in different ecosystem components (e.g., above- and belowground components) under management (e.g., from light thinning to clear cutting) to get an overview of stock variation. Different management practices (e.g., livestock and thinning) under silvopastoral systems should consider a balance between provisioning, other ecosystem services, and biodiversity (Martínez Pastur et al. 2021, 2022).

Studies on forest carbon stocks are mainly based on estimates of aboveground biomass (trees, shrubs, and grasses) or only living woody stems, without considering other compartments (e.g., soil layer) and different stages of decomposition (e.g., litter, CWD, or standing dead trees), so the scopes of estimates are often diffused (Houghton et al. 2009). Also, several studies estimate carbon concentration as 50% of dry weight biomass without differentiating tree compartments (Aalde et al. 2006), which may lead to under- or overestimates (Martin et al. 2018). Some studies in *N. antarctica* forests estimate biomass and carbon content (Peri et al. 2006, 2008, 2010; Gargaglione et al. 2010), although they do not include all stand components (e.g., soil layer).

The objective of this work was to quantify the natural variation of the carbon storage (t C ha^{-1}) in *N. antarctica* forests (natural and under management). With this research, we wanted to answer (i) what is the relative importance of each carbon storage component in the different forest landscapes? (ii) What is the magnitude of carbon storage variation in different forest components according to the natural stages or human-derived impacts? We hypothesised that the variation of carbon storage among the different phases of natural forests does not greatly change, which defines the natural stability of the ecosystem. Moreover, carbon storage decreases with the magnitude of human-derived impacts (harvesting or fire), mainly by affecting the aboveground components.

Materials and methods

Data taking and measurements

The study area encompasses most of the natural distribution of ñire forests in the Argentinian side of Tierra del Fuego (53°38′–54°37′S, 66°28′–68°36′ W) (Fig. A1). The forest area of the province was estimated using the National Forest Inventory developed by the Dirección Nacional de Bosques (2021) and the Global Forest Change data (Hansen et al. 2013). Our sampling included 145 locations (stands or open land areas) of both even- and uneven-aged *N. antarctica* forests and associated environments (>2 ha each) that grow on both Vertisol and Inceptisol soil types. The framework of the study was previously described by Martínez Pastur et al. (2021), considering natural forests with different tree age structures (i) unmanaged even-aged stands: 20–40 years old with an average of basal area (BA) of 23.7 m^2 ha^{-1} and a dominant height (DH) of 9.1 m (n = 4, initial growth phase (IGP)), 40–80 years old with BA = 43.0 m^2 ha^{-1} and DH = 10.6 m (n = 6, final growth phase (FGP)), 80–120 years old with BA = 31.9 m^2 ha^{-1} and DH = 9.2 m (n = 12, mature, MAT), and >120 years old with BA = 42.2 m^2 ha^{-1} and DH = 10.1 m (n = 5, decay, DEC). (ii) Unmanaged uneven-aged stands: young uneven-aged (YUA) mixing IGP and FGP phases (n = 11 stands with BA = 34.6 m^2 ha^{-1} and DH = 8.6 m) and mature uneven-aged (MUA) mixing MAT and DEC phases (n = 9 stands with BA = 33.3 m^2 ha^{-1} and DH = 8.9 m). We selected two controls for comparisons, MAT because it is the climax stage and FGP because it is the main structure selected for thinning. (iii) Harvested stands were classified according to cut intensity, low intensity (LH) when remnant BA was >30 m^2 ha^{-1} (n = 27 stands), high intensity (HH) when BA was between 5 and 30 m^2 ha^{-1} (n = 31 stands), and clear-cuts (CC) when remnant BA was <5 m^2 ha^{-1} (n = 9 stands). (iv) Finally, we included transformed and associated environments, fired forests (FIRE) (n = 8 areas with BA = 16.2 m^2 ha^{-1} and DH = 10.2 m), forest edges with open lands (FER) (n = 13 areas), dry grasslands (OPD) (n = 6 areas), and humid grasslands (OPH) (n = 4 areas) (Fig. A1). For more details on these stands see Martínez Pastur et al. (2020, 2021, 2022).

We randomly placed a 50 m transect to characterise each site in mid-summer (January and February). To calculate total biomass accumulation at each stand, we obtained the following variables: individual development phases of trees (Fig. A1), diameter at breast height (DBH) of trees >5 cm, DH to calculate site quality (Veblen et al. 1996) of the stands, tree density, BA, total over-bark volume (TOBV), and overstory canopy cover (OC, %). We measured the density of the advanced regeneration (AR) (>1.3 m height and <5.0 cm DBH), its BA–RA, and total over-bark volume (TOBV–AR). We characterised the forest floor, including the CWD and aboveground biomass (seedlings and understory vascular plants). Four soil samples (0-10 cm depth) were randomly taken along each transect using a field borer with known volume (230.9 cm^3) after previously removing the litter layer. Samples were weighted before and after air drying in laboratory conditions (24 °C) until constant weight. Soil bulk density (SBD, t m^3) was obtained from the average of the four samples (soil weight over bored volume). Coarse root debris (>2 mm) and soil aggregates (e.g., small stones and large sand-sized) were separated from the soil samples by sieving (Martínez Pastur et al. 2021; Chaves et al. 2023). From this separated material, the proportion of fine roots and woody debris in the soil was calculated. For chemical analyses, we pooled individual soil samples into one combined sample per stand. Each sample was finely ground to below 2 mm using a tungsten–carbide mill, and then was determined total organic carbon (OM, %) from soil samples washed with HCl (50%). Data for C content were presented as kg m^2 in the first 30 cm depth, using the SBD data of each stand (Martínez Pastur et al. 2021).

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Table 1. Components of a forest ecosystem considered for carbon storage assessment according to biomass allocation and categories (adapted from Chaves et al. 2023).

Category	Location	Component	Acronym
(A) Trees	Aboveground	Leaves	LEA
		Branches	BRA
		Bark	BAR
		Wood	WOO
	Belowground	Coarse roots	COR
		Fine roots	FIR
(B) Deadwood	Aboveground	Coarse woody debris	CWD
		Dead trees	DET
	Belowground	Coarse roots of dead trees	CRT
		Woody debris in soil	WDS
(C) Understory plants	Aboveground	Alive understory plants	AUP
		Dead understory plants	DUP
(D) Soil layer	Belowground	Litter	LIT
		Soil	SOI

Note: Copyright © 2023; Chaves et al. (2023).

Assumptions and carbon content modelling

A total of 14 different above- and belowground components were used to estimate the carbon content (Table 1), sorted by trees, deadwood, understory plants, and soil layer. For (A) trees, we considered: TOBV of live trees was disaggregated into three aboveground components (WOO = wood, BAR = bark, and BRA = branches), while coarse roots (COR) were estimated as a proportion of TOBV following Peri et al. (2006, 2008). Volume was transformed in biomass using wood density (0.66 kg m^3) (Dettmann et al. 2013), while carbon content was estimated following Peri et al. (2010). Stand-level data (t C ha^{-1}) were obtained using forest inventory plots. Leaves (LEA) were calculated based on litter production, based on BA and stand age following Soler et al. (2015); 0.038 t m^{-2} BA (MAT, DEC, MUA), 0.073 t m^{-2} BA (IGP, FGP, YUA, AR), and 0.045 t m^{-2} BA for disturbed stands. Carbon content was obtained following Peri et al. (2010). Fine roots (FIR) biomass was determined from sieved soil samples and borer volume, and carbon content following Peri et al. (2010). Data were presented at stand level (t C ha^{-1}).

For (B) deadwood we considered; dead coarse roots (CRT) and dead tree stems (DET) using TOBV of dead trees, root proportions in relation to development stage and site quality (Gargaglione et al. 2010), wood density (Dettmann et al. 2013), and carbon concentration of live trees (Peri et al. 2010). Volume of CWD was transformed into biomass, including a decay rate estimated using other *Nothofagus* species (Carmona et al. 2002); 55.6% in natural forests and 65.8% in impacted stands. The volume was transformed in biomass as described before. Woody debris in soil (WDS) was determined using sieved soil samples for the first 30 cm soil layer, and stand-level values were obtained (t C ha^{-1}).

For (C and D) understory plants and soil layer values; understory biomass (alive (AUP) and dead (DUP)) were converted to carbon content (t C ha^{-1}) following Peri and Lasagno (2010). Litter (LIT) inputs and decomposition rate following Bahamonde et al. (2012). The resulting values represent a litter biomass of ×3.98 annual leaf production in dense forests, and ×2.21 in impacted areas. Resulting biomass was converted in carbon concentration following Peri et al. (2010) and converted to stand level (t C ha^{-1}). The organic matter (OM) was transformed in organic carbon (SOI) using a relationship with values obtained from an automatic analyser (LECO CR12, USA). Field values were transformed assuming a decay rate along the soil profile and increasing SBD (data not shown obtained from $n = 80$ samples). Finally, SOI was multiplied by SBD to obtain soil carbon content (t ha^{-1}) for the first 30 cm depth.

Statistical analyses

Treatments were compared using uni- and multivariated analyses, considering three levels (i) natural dynamics of the forests (IGP, FGP, YUA, MUA, MAT, DEC), (ii) harvesting (LH, HH, CC) versus controls (FGP, MAT), and (iii) transformed and associated environments (FIRE, FER, OPD, OPH) versus controls with the aim of visualising changes in C storage between natural environments and environments subjected to different degrees of conversion. We performed one-way ANOVAs to analyse the differences in carbon content (t C ha^{-1}) of the treatments by conversion (see Table 1) by Fisher's and Tukey's tests at $P < 0.05$. We also performed principal component analysis (PCA) to quantify the similarity among plots according to the carbon content of the studied components. We split the comparisons considering natural dynamics of the forest, harvesting, and transformed and associated environments. We set up PCA to calculate intercolumn correlation coefficients for the cross-product matrix and assessed the significance of each axis with Monte Carlo permutation tests ($n = 999$). We also evaluated differences among groups using multiresponse permutation procedures (MRPP) with Bray–

Table 2. ANOVAs for carbon storage categories (t C ha $^{-1}$) (trees, deadwood, understory plants, and soil layer) in a *Nothofagus antarctica* forest ecosystem, considering different treatments and forest phases.

Treatments	Phase	Total	Trees	Deadwood	Understory plants	Soil layer
Natural cycle	IGP	295.92ab	89.62 (30.3%)	15.45a (5.2%)	0.23 (0.1%)	190.61 (64.4%)
	FGP	343.85ab	121.83 (35.4%)	34.39ab (10.0%)	0.36 (0.1%)	187.28 (54.5%)
	YUA	289.28a	93.84 (32.4%)	36.07ab (12.5%)	0.67 (0.2%)	158.69 (54.9%)
	MUA	331.26ab	101.27 (30.6%)	56.44bc (17.0%)	0.77 (0.2%)	172.77 (52.2%)
	MAT	328.40ab	95.52 (29.1%)	59.74bc (18.2%)	0.78 (0.2%)	172.37 (52.5%)
	DEC	385.89b	131.10 (34.0%)	74.59c (19.3%)	0.83 (0.2%)	179.37 (46.5%)
	F(*p*)	*2.49(0.04)*	*1.79(0.14)*	*7.72(<0.01)*	*1.33(0.27)*	*0.61(0.70)*
Harvesting	FGP	343.85d	121.83c (35.4%)	34.39a (10.0%)	0.36a (0.1%)	187.27c (54.5%)
	MAT	328.40 cd	95.52bc (29.1%)	59.74b (18.2%)	0.78a (0.2%)	172.37bc (48.9%)
	LH	284.37bc	109.43c (38.5%)	37.80a (13.3%)	0.61a (0.2%)	136.52a (48.0%)
	HH	244.68b	66.19b (27.1%)	31.50a (12.9%)	0.90ab (0.4%)	146.10ab (59.7%)
	CC	187.06a	12.05a (6.4%)	27.88a (14.9%)	1.58b (0.8%)	145.56ab (77.8%)
	F(*p*)	*22.31(<0.01)*	*32.01(<0.01)*	*5.64(<0.01)*	*5.53(<0.01)*	*5.27(<0.01)*
Transformed and associated environments	FGP	343.85b	121.83b (35.4%)	34.39b (10.0%)	0.36 (0.1%)	187.27b (54.5%)
	MAT	328.40b	95.52b (29.1%)	59.74b (18.2%)	0.78 (0.2%)	172.37ab (52.5%)
	FIRE	184.46a	30.96a (16.8%)	36.28b (19.7%)	0.86 (0.5%)	116.36a (63.1%)
	FER	124.71a	2.68a (2.1%)	1.32a (1.1%)	1.18 (0.9%)	119.53a (95.8%))
	OPD	127.54a	0.00a (0.0%)	0.92a (0.7%)	1.48 (1.2%)	125.14ab (98.1%)
	OPH	157.80a	0.00a (0.0%)	0.55a (0.3%)	1.38 (0.9%)	155.86ab (98.8%)
	F(*p*)	*40.64(<0.01)*	*51.41(<0.01)*	*14.95(<0.01)*	*2.18(0.07)*	*4.95(<0.01)*

Note: F = Fisher's test, p = probability. Different letters show significant differences in means using Tukey's test at $P < 0.05$. The percentage contribution of each component to the total carbon storage is presented in parentheses. FGP and MAT were control treatments.

Table 3. ANOVAs for carbon storage (t C ha^{-1}) of tree category components (LEA = leaves, BRA = branches, BAR = bark, WOO = wood, COR = coarse roots, and FIR = fine roots) in a *Nothofagus antarctica* forest ecosystem, considering different treatments and forest phases.

		Trees					
Treatments	Phase	LEA	BRA	BAR	WOO	COR	FIR
Natural cycle	IGP	1.40c (1.6%)	4.91ab (5.5%)	8.65 (9.7%)	36.09 (40.3%)	25.66ab (28.6%)	12.91a (14.4%)
	FGP	1.55c (1.3%)	6.91b (5.7%)	12.54 (10.3%)	53.20 (43.7%)	36.06b (29.6%)	11.56a (9.5%)
	YUA	1.33bc (1.4%)	4.46ab (4.8%)	9.19 (9.8%)	41.62 (44.3%)	22.91ab (24.4%)	14.34ab (15.3%)
	MUA	0.67a (0.7%)	4.38ab (4.3%)	10.38 (10.2%)	49.88 (49.3%)	22.09ab (21.8%)	13.87ab (13.7%)
	MAT	0.66a (0.7%)	4.08a (4.3%)	9.53 (10.0%)	45.51 (47.6%)	20.62a (21.6%)	15.12ab (15.8%)
	DEC	0.89ab (0.7%)	5.65ab (4.3%)	13.28 (10.1%)	63.57 (48.5%)	28.57ab (21.8%)	19.13b (14.6%)
	F(*p*)	*14.75(<0.01)*	*2.78(0.03)*	*1.62 (0.18)*	*1.76(0.14)*	*3.06(0.01)*	*2.58(0.04)*
Harvesting	FGP	1.55e (1.3%)	6.91d (5.7%)	12.54c (10.3%)	53.20c (43.7%)	36.06d (29.6%)	11.56ab (9.5%)
	MAT	0.66c (0.7%)	4.08bc (4.5%)	9.53c (10.3%)	45.51c (49.3%)	20.62bc (22.5%)	15.12b (12.6%)
	LH	0.90d (0.8%)	5.30 cd (4.8%)	11.59c (10.6%)	53.89c (49.3%)	27.05c (24.7%)	10.69ab (9.8%)
	HH	0.39b (0.6%)	2.44b (3.7%)	5.50b (8.3%)	25.90b (39.1%)	12.39b (18.7%)	19.57c (29.6%)
	CC	0.04a (0.3%)	0.20a (1.7%)	0.46a (3.8%)	2.17a (18.0%)	1.04a (8.6%)	8.13a (67.5%)
	F(*p*)	*78.37(<0.01)*	*33.40(<0.01)*	*33.63(<0.01)*	*32.61(<0.01)*	*33.16(<0.01)*	*27.22(<0.01)*
Transformed and associated environments	FGP	1.55c (1.3%)	6.91c (5.7%)	12.54b (10.3%)	53.20b (43.7%)	36.06c (29.6%)	11.56c (9.5%)
	MAT	0.66b (0.7%)	4.08b (4.3%)	9.53b (10.0%)	45.51b (47.6%)	20.62b (21.6%)	15.12c (15.8%)
	FIRE	0.23a (0.7%)	1.13a (3.7%)	2.52a (8.1%)	11.82a (38.2%)	5.75a (18.6%)	9.50bc (30.7%)
	FER	0.01a (0.4%)	0.02a (0.7%)	0.04a (1.5%)	0.15a (5.6%)	0.11a (4.1%)	2.37ab (87.8%)
	OPD	0.00a (0.0%)	0.00a (0.0%)	0.00a (0.0%)	0.00a (0.0%)	0.00a (0.0%)	0.00a (0.0%)
	OPH	0.00a (0.0%)	0.00a (0.0%)	0.00a (0.0%)	0.00a (0.0%)	0.00a (0.0%)	0.00a (0.0%)
	F(*p*)	*96.02(<0.01)*	*55.85(<0.01)*	*46.59(<0.01)*	*43.00(<0.01)*	*57.07(<0.01)*	*13.12(<0.01)*

Note: F = Fisher's test, p = probability. Different letters show significant differences in means using Tukey's test at $P < 0.05$. The percentage contribution of each component to the total carbon storage is presented in parentheses. FGP and MAT were control treatments.

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Table 4. ANOVAs for carbon storage (t C ha^{-1}) of deadwood category components (CWD = coarse woody debris, DET = dead trees, CRT = coarse roots of dead trees, and WDS = woody debris in soil) in a *Nothofagus antarctica* forest ecosystem, considering different treatments and forest phases.

Treatments	Phase	Deadwood			
		CWD	DET	CRT	WDS
Natural cycle	IGP	13.63 (88.2%)	1.32a (8.5%)	0.44a (2.8%)	0.06a (0.4%)
	FGP	13.69 (39.8%)	4.40a (12.8%)	1.46a (4.2%)	14.85bc (43.2%)
	YUA	13.68 (37.9%)	8.87ab (24.6%)	2.94ab (8.2%)	10.58b (29.3%)
	MUA	16.55 (29.3%)	15.62ab (27.7%)	5.18ab (9.2%)	19.10c (33.8%)
	MAT	17.28 (28.9%)	22.04b (36.9%)	7.30b (12.2%)	13.11bc (21.9%)
	DEC	20.73 (27.8%)	13.42ab (18.0%)	4.45ab (6.0%)	35.99d (48.3%)
	F(p)	*0.41(0.84)*	*4.58(<0.01)*	*4.58(<0.01)*	*44.62(<0.01)*
Harvesting	FGP	13.69 (39.8%)	4.40a (12.8%)	1.46a (4.2%)	14.85c (43.2%)
	MAT	17.28 (30.9%)	22.04b (38.7%)	7.30b (12.8%)	13.11c (17.6%)
	LH	18.85 (49.9%)	9.24a (24.5%)	3.06a (8.1%)	6.64b (17.6%)
	HH	15.92 (50.5%)	10.59ab (33.6%)	3.51ab (11.1%)	1.48a (4.7%)
	CC	19.89 (71.4%)	5.35a (19.2%)	1.77a (6.4%)	0.86a (3.1%)
	F(p)	*0.43(0.79)*	*5.30(<0.01)*	*5.30(<0.01)*	*148.61(<0.01)*
Transformed and associated environments	FGP	13.69ab (39.8%)	4.4a (12.8%)	1.46a (4.2%)	14.85c (43.2%)
	MAT	17.28b (28.9%)	22.04b (36.9%)	7.30b (12.2%)	13.11c (21.9%)
	FIRE	13.75ab (37.9%)	12.82ab (35.3%)	4.25ab (11.7%)	5.46b (15.0%)
	FER	0.06a (4.5%)	0.00a (0.0%)	0.00a (0.0%)	1.26a (95.5%)
	OPD	0.00a (0.0%)	0.00a (0.0%)	0.00a (0.0%)	0.92a (100.0%)
	OPH	0.00a (0.0%)	0.00a (0.0%)	0.00a (0.0%)	0.55a (100.0%)
	F(p)	*5.94(<0.01)*	*7.62(<0.01)*	*7.62(<0.01)*	*53.38(<0.01)*

Note: *F* = Fisher's test, *p* = probability. Different letters show significant differences in means using Tukey's test at $P < 0.05$. The percentage contribution of each component to the total carbon storage is presented in parentheses. FGP and MAT were control treatments.

Curtis distances. We used *T* statistic to evaluate differences. Multivariate analyses were performed with PC-ORD 5.0.

Results

Natural cycle

Total carbon significantly increased with forest age, from 289 to 386 t C ha^{-1} (Table 2). These differences are related to deadwood category; however, it accounts for only a small percentage of total carbon (5%–19%). The higher accumulation was in soil layer (47%–64%) and trees (29%–35%) categories (Fig. A2). The contribution of tree components followed WOO > COR > FIR > BAR > BRA > LEA (Table 3). LEA and COR decreased with stand age, while BRA and FIR increased. Deadwood components (Table 4) varied according to the forest types, where DET, CRT, and WDS increased with forest age. Understory plants (AUP and DUP) showed no significant differences, while LIT decreased with forest age (Table 5).

Total belowground carbon content (Fig. 1A) was significantly higher than aboveground for all treatments in the natural cycle. Moreover, aboveground increased with age (66–118 t C ha^{-1}), whereas belowground did not change among treatments (230–268 t C ha^{-1}). PCA (Fig. 2A) showed that even-aged young forests at IGP and FGP, respectively and YUA formed a close group due to LEA and LIT. This group is separated from MAT, DEC, and uneven-aged stands with MUA, mainly due to the WOO and BAR components. For the first two axes, eigenvalues were 4.946 ($P = 0.001$) and 3.185 ($P = 0.001$), explaining 35.3% and 22.7% of total variance. Axis 1 was explained by COR > BRA > BAR > LIT > LEA > WOO, while Axis 2 was related to DET = CRT > WOO > WDS (Table A2). MRPP showed the similarities among treatments (Table A3), with no differences among young stands (IGP, FGP, and YUA), but with differences in older stands (MAT and DEC). Uneven-aged stands (YUA and MUA) presented differences compared to even-aged stands.

Harvesting

Carbon contents (Table 2) in harvested stands varied significantly as a function of the intensity of the intervention, being lower than those of the controls treatments; FGP and MAT phase. LH harvests maintained 84.6% of total carbon content compared to controls, while HH harvests retained 72.8%, and CC harvests retained only 55.7%. Compartmentalization varied greatly among treatments (Fig. A2), e.g., soil is the main component of CC harvesting. In general, carbon content decreased with harvesting intensity (trees, deadwood, and soil layer categories), while for the understory plant categories, it increased, as did the tree components of the remnant trees (Table 3). The contribution of each component follows the same pattern as described before, except in the case of clear cuttings, where FIR becomes more relevant due to the higher number of understory plants and regeneration. For deadwood category (Table 4), carbon content of CRT

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Table 5. ANOVAs for carbon storage (t C ha $^{-1}$) of understory plants category components (AUP = alive understory plants and DUP = dead understory plants) and soil layer category components (LIT = litter and SOI = soil) in a *Nothofagus antarctica* forest ecosystem, considering different treatments and forest phases.

		Understory plants		Soil layer	
Treatments	Phase	AUP	DUP	LIT	SOI
Natural cycle	IGP	0.17 (73.9%)	0.06 (26.1%)	5.57c (2.9%)	185.04 (97.1%)
	FGP	0.28 (77.8%)	0.08 (22.2%)	6.17c (3.3%)	181.09 (96.7%)
	YUA	0.38 (56.7%)	0.29 (43.3%)	5.29bc (3.3%)	153.39 (96.7%)
	MUA	0.45 (58.4%)	0.32 (41.6%)	2.68a (1.6%)	170.09 (98.4%)
	MAT	0.45 (58.4%)	0.32 (41.6%)	2.64a (1.5%)	169.73 (98.5%)
	DEC	0.49 (59.8%)	0.33 (40.2%)	3.55ab (2.0%)	175.82 (98.0%)
	F(*p*)	*0.77(0.57)*	*1.96(0.11)*	*14.70(<0.01)*	*0.60(0.70)*
Harvesting	FGP	0.28a (77.8%)	0.08a (22.2%)	6.17e (3.3%)	181.09b (96.7%)
	MAT	0.45a (53.7%)	0.32bc (46.3%)	2.64d (1.9%)	169.73ab (98.1%)
	LH	0.38a (62.3%)	0.23ab (37.7%)	2.00c (1.4%)	134.53a (98.5%)
	HH	0.60ab (66.7%)	0.30ab (33.3%)	0.85b (0.6%)	145.25a (99.4%)
	CC	1.04b (65.8%)	0.54c (34.2%)	0.10a (0.1%)	145.46ab (99.9%)
	F(*p*)	*4.50(<0.01)*	*5.83(<0.01)*	*157.14(<0.01)*	*4.59(<0.01)*
Transformed and associated environments	FGP	0.28 (77.8%)	0.08 (22.2%)	6.17c (3.3%)	181.09b (96.7%)
	MAT	0.45 (58.4%)	0.32 (41.6%)	2.64b (1.5%)	169.73ab (98.5%)
	FIRE	0.56 (65.1%)	0.30 (34.9%)	0.51a (0.4%)	115.84a (99.6%)
	FER	0.92 (78.0%)	0.26 (22.0%)	0.01a (0.0%)	119.52ab (100.0%)
	OPD	1.08 (73.0%)	0.40 (27.0%)	0.00a (0.0%)	125.14ab (100.0%)
	OPH	0.99 (71.2%)	0.40 (28.8%)	0.00a (0.0%)	155.86ab (100.0%)
	F(*p*)	*2.49(0.05)*	*1.61(0.18)*	*134.61(<0.01)*	*4.34(<0.01)*

Note: F = Fisher's test, p = probability. Different letters show significant differences in means using Tukey's test at $P < 0.05$. The percentage contribution of each component to the total carbon storage is presented in parentheses. FGP and MAT were control treatments.

and WDS decreased with harvesting intensity. DET also presented significant differences, being higher in control (MAT) and HH harvests compared to young forests (FGP). The contribution of components varied with harvesting intensity (Fig. A2), where CWD in heavy cuts (e.g., HH and CC) became the main contributor, and WDS decreased. Understory plant (AUP and DUP) carbon content increased with harvesting intensity, while soil layer components (LIT and SOI) decreased significantly with cutting intensity (Table 5). Belowground carbon content was significantly higher than aboveground carbon content (Fig. 1B) for all treatments (controls and harvested) and decreased with harvesting intensity.

PCA found a clear separation of treatments (Fig. 2B), where Axis 1 is correlated with intervention intensity (FGP, MAT, LH, HH, and CC, ordered from left to right), and Axis 2 with stand age. Eigenvalues were 6.264 ($P = 0.001$) for Axis 1 and 2.162 ($P = 0.001$) for Axis 2, explaining 44.7% and 11.4% of total variance, respectively. Axis 1 was correlated with BRA > COR > BAR > LEA > WOO > LIT, and Axis 2 with DET = CRT > DUP (Table A2). MRPP reinforced PCA results, showing significant differences among all harvested and controls (Table A3).

Transformed forests and associated environments

Disturbed forests, such as burned forests (FIRE) and forest edges with regeneration (FER), did not differ in carbon content from open lands, neither dry (OPD) nor humid (OPH), resulting in lower accumulations than controls (FGP and MAT) (Table 2). Natural OPD contained 37.9% and OPH 46.9% of the total carbon content compared to controls, while transformed forests had intermediate (54.9% for FIRE) or similar values (37.1% for FER) (Fig. A2). Tree category (Table 2) showed intermediate values in transformed forests, whereas deadwood category was split into two groups (controls and FIRE compared to FER and open lands). Understory plant category did not vary, while soil layer had the lowest values (<120 t C ha^{-1}) in transformed forests compared to grasslands (125–155 t C ha^{-1}) and controls (>170 t C ha^{-1}). Trees and deadwood components displayed differences (Tables 3 and 4), where transformed forests had intermediate values between controls (maximum values) and open lands (minimum values). Understory plant category did not differ among treatments, while soil layer showed significant differences (LIT and SOI) (Table 5). LIT changed among controls and other treatments, where transformed forests (FIRE, FER) indicated intermediate values (transformed forests > open grasslands). SOI in transformed forests had the lowest values (FER > FIRE). The contribution of above- and belowground (Fig. 1C) shows that the carbon content of below- was higher than aboveground in all treatments. However, aboveground split between controls and fires/open lands (FER > OPD = OPH), while belowground was higher in controls (FGP and MAT) than the rest. PCA showed a clear separation among treat-

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ments (Fig. 2C). Axis 1 was correlated with degree of transformation (e.g., controls to the left, intermediate values for FIRE, and intermingled group for other treatments). Axis 2 is related to stand age. Eigenvalues and probabilities were 8.144 and $P = 0.001$, and 2.007 and $P = 0.005$ for Axes 1 and 2, explaining 58.2% and 14.3% of variance. Axis 1 was correlated with BAR > BRA > WOO > COR > WDS > LEA > LIT, and Axis 2 with DET = CRT > CWD (Table A2). MRPP reinforced PCA results, showing differences among different categories (Table A3).

Discussion

Carbon content across the natural cycle of unmanaged forests

Nothofagus antarctica forests follow simple gap dynamics across lifespan, and regeneration (seeds and root-sprouting) reacts to the opening of the OC (Peri et al. 2022). This dynamic path leads to even- or uneven-aged stands with more than 200 years old (see Fig. A1). We found differences in carbon contents along stand age with differences >25% between young and mature stands. Thompson et al. (2009) also indicated that carbon stocks are larger in old forests. These differences were mainly related to deadwood, while other categories remained without differences. Law et al. (2002) determined larger amount of carbon in mature *Pinus ponderosa* stands (45–250 years old) compared to young ones (14 years old), where differences were due to wood accumulation, and contrary to our results, to deadwood in young stands. Peri et al. (2010) determined for *N. antarctica* that not only stand age influenced the compartmentalization of carbon content, but also site quality and OC. Our results presented no differences between young and old stands for each tree category, due to a compensation at the stand level between young forests represented by dense stands with full canopy cover (e.g., higher BA and litter) and old stands that presented large trees but open canopies with natural dieback (e.g., more understory plants and fine root in soils) (Martínez Pastur et al. 2020). However, an influence of tree size (Stephenson et al. 2014) was detected when comparing tree-specific components (Table 3), e.g., coarse roots, branches, and leaves (Landsberg and Gower 1997; Peri et al. 2010). Our results are consistent with Nyirambangutse et al. (2017), who reported that total net production in tropical forests was similar for different successional stages balancing aboveground components (higher in late stages) and growth rate (higher in early stages). Besides, the increase in deadwood across development stages can be explained for self-thinning tree mortality and low decomposition rate at higher latitudes (Carmona et al. 2002; Bahamonde et al. 2012). Deadwood was also related to stand age, e.g., bark and wood integrated in soils, or dead trees in overstory (e.g., snags) (Landsberg and Gower 1997; Martínez Pastur et al. 2021).

In terms of ecosystem stability (resistance and resilience) (Harrison 1979), belowground contents did not change between even- and uneven-aged stands or among developmental stages (Fig. 1A) (differences of 17%). Wang et al. (2020) reported that soil carbon decreased with stand age in mixed forests in China, while Ouyang et al. (2017) reported an increase, indicating that forest succession enhances concentration and storage. The main differences in carbon storage were detected in aboveground components, especially with those related to stand dynamics (33% difference). Similarly, Wang et al. (2020) reported that above- and belowground carbon storage had a positive correlation with age. Here, soil is the main proxy of stand resilience for natural impacts, while tree category seems resilient to harvesting impacts allowing for the persistence of ecosystems. Several authors reported that old-growth forests are more resilient and resistant to changes compared with artificial forests (e.g., Thompson et al. 2009). However, this carbon balance is not stable over time in natural ecosystems and can be affected by natural factors, e.g., Zhou et al. (2006) showed an increase in

Fig. 1. ANOVAs for total carbon storage (t C ha-1) considering treatments ((A) natural cycle, (B) harvesting, and (C) transformed and associated environments) and forest phases, classified according to above- (light colours) and belowground (dark colours) components. FGP and MAT were control treatments (green bars). Capital letters indicate significant differences by Tukey's test ($P < 0.05$) between above- and belowground, while lowercase letters indicate differences among forest phases. Fisher's test and probability are in Table A1.

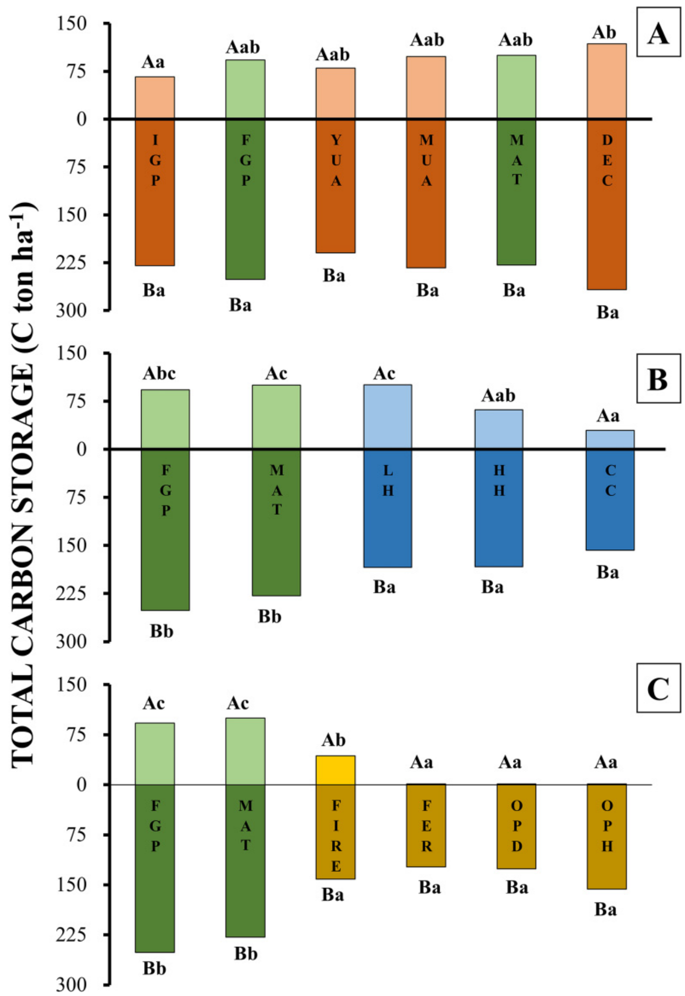

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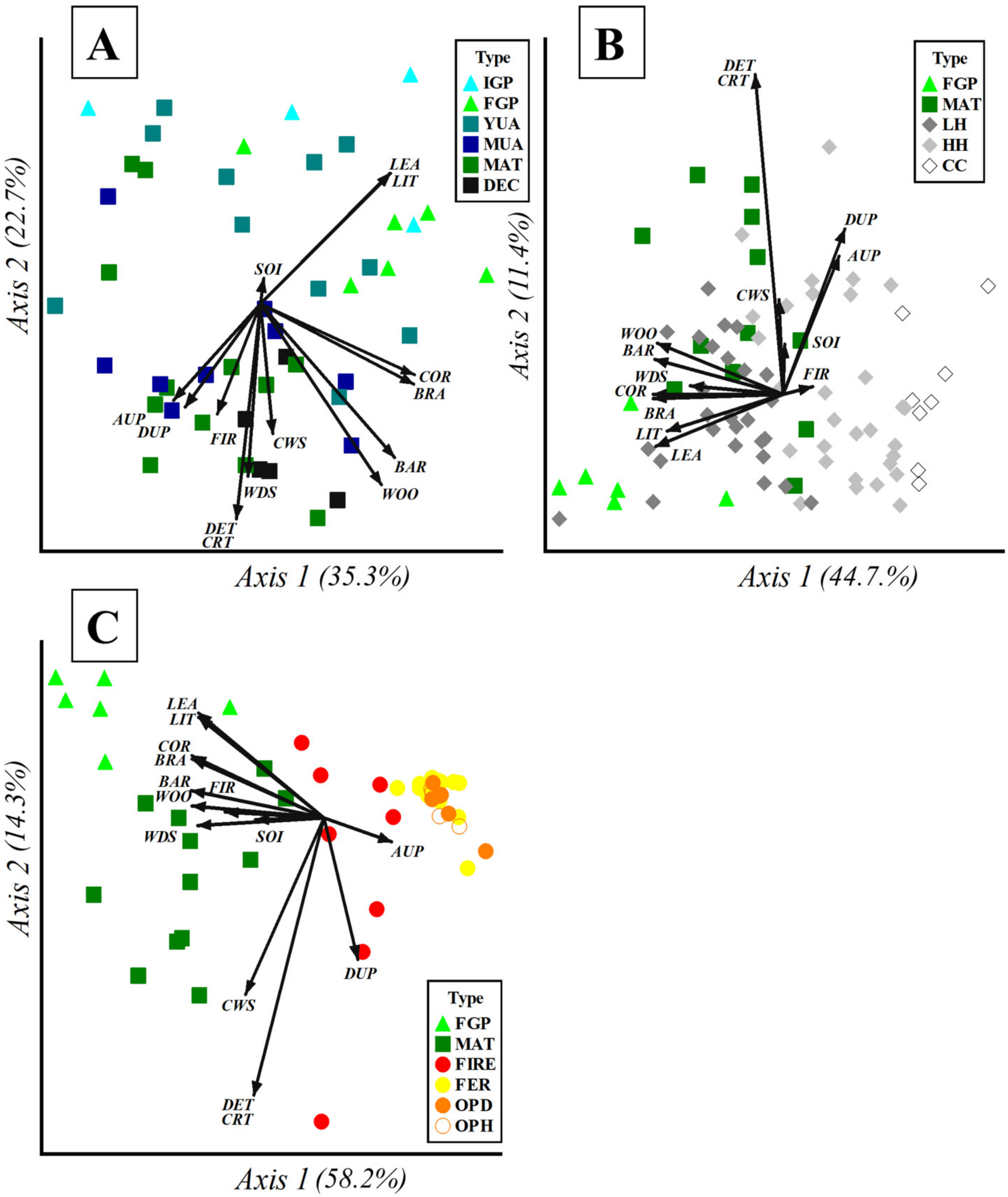
Fig. 2. PCA for carbon storage (t C ha^{-1}) considering treatments ((A) = natural cycle, (B) = harvesting, and (C) = transformed and associated environments) and controls (FGP and MAT, green dots) (see acronyms in Fig. A1 and Table 1). Importance of each component is in Table A2.



soil carbon (0.035% per year) in old-growth stands in China (1973–2003).

FCM: from thinning to land-use conversion

Few studies have investigated above- and belowground carbon pools in *Nothofagus* forests (e.g., Caldentey 1992) to understand the impacts of harvesting (Hart et al. 2003). Management proposals for Patagonia range from selective cuts to CC to maximise livestock grazing (Manacorda and Bonvissuto 2001). Silvopastoral systems provides a balance between provision and other ecosystem services (Peri et al. 2022) and coincides with the objectives of the FCM (Birdsey et al. 2000) increasing ecosystem services from monetary provision and reducing carbon losses (Ameray et al. 2021). According to

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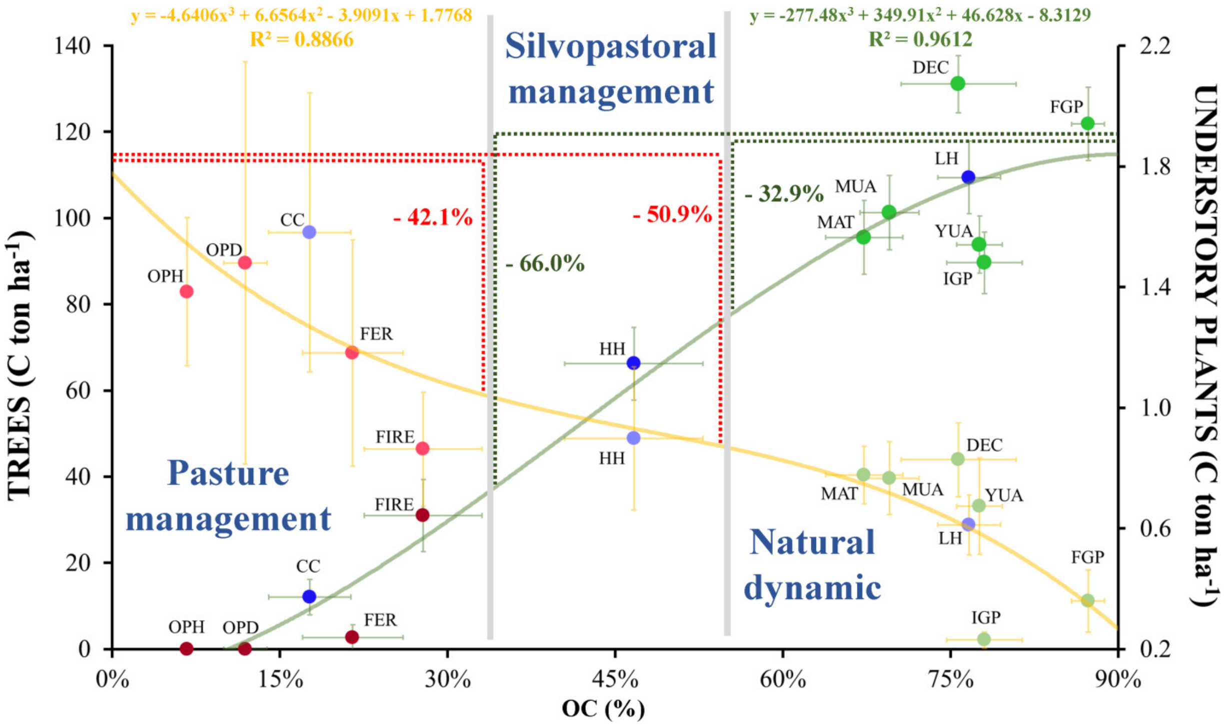
Fig. 3. Forest carbon management in silvopastoral systems: carbon content (t C ha^{-1}) of trees (dark dots and green line) and understory plants (pale dots and yellow line) in relation to crown cover of overstory (OC, %) (see Table 1) according to forest treatments (natural cycle in green dots, harvesting in blue dots, and transformed and associated environments in red dots) (see Fig. A1). Bars indicate the standard error of estimation on both axes. Lines indicate decreasing maximum values, which define thresholds (grey lines) for the tree categories (dark green dotted lines) and understory plants (red dotted lines). R-squared and function are presented on the same-coloured lines.



our results, forests growing under natural dynamics increase carbon content with age. Thus, mature forests (even- and uneven-aged) had higher carbon stock values. Compared to open lands, natural forests had a higher carbon content ×2.1–×2.6. In contrast, open lands increased plant biomass by ×2.4–×2.6 compared to control natural forests. However, understory plants represent a small percentage of carbon content (0.1%–0.2% in controls and 0.9%–1.2% in open lands). Carbon content is directly affected by harvesting intensity, with negative and positive synergies (Martínez Pastur et al. 2021, 2022). Harvesting reduced carbon content by up to 85% in low-intensity harvesting and 56% in clear-cutting compared to controls, but only the most intensive harvesting increased the understory.

The challenge to design new management alternatives

Management proposals are based on monetary ecosystem services according to markets (Chillo et al. 2021), without considering trade-offs and resilience of natural ecosystems (Drever et al. 2006). Recently, management proposals have included multiple objectives, both monetary and non-monetary (Peri et al. 2022). In Patagonia, undisturbed natural forests conserve most of the carbon stocks (Fig. 3). The proposed management removed most of the overstory tree canopy cover (<35% OC = burned and CC forests) and promoted maximum development of understory plants, yet carbon stocks were significantly reduced. One approach to maintaining forest integrity, and consequently carbon stocks, is to combine multiple management objectives (Bussoni et al. 2021). Silvopastoral systems enhance pasture compared to natural forests (OC between 35% and 55%) and maintain the integrity of natural legacies, allowing for increased forest resilience (Peri et al. 2022). However, soil carbon was affected by management (e.g., tree removal, soil compaction, or increased radiation) leading to short-term losses (Turner and Lambert 2000). Silvopastoral systems stock less tree biomass than natural forests (32.9%–66.0%) due to harvesting, producing more herbaceous biomass (42.1%–50.9%) (Fig. 3). Martínez Pastur et al. (2021) highlighted that harvesting intensity thresholds are required to determine sustainable management. Low-intensity thinning could be an alternative with synergistic characteristics, improving tree growth, enhancing natural regeneration, and forage production (Yanai et al. 2003). This management strategy is compatible with the FCM (Bravo et al. 2017) by improving carbon sequestration in managed stands. In fact, the Food and Agriculture Organization considers silvopastoral system as one climate-smart agricultural practice that provides economic diversity and ecosystem protection (Harvey et al. 2014).

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Conclusions

Modelling carbon stocks in natural and managed stands using many variables provided accurate estimates. Carbon estimates classified into different above- and belowground components allowing us to determine changes in the natural cycle and the impacts of management. Moreover, we integrated important components of ecological cycles (e.g., litter), which have been neglected in traditional studies. Natural forests differed in their structure. However, carbon stocks did not vary greatly rather, the differences were related to the age of the stand. Management proposals had a strong influence on carbon stocks, where silvopastoral systems allowed a balance to be found between several objectives (e.g., maintenance of carbon stocks in managed stands). Harvesting in silvopastoral systems results in more resilient stands, where losses were minimised (e.g., maintaining carbon stocks and improving economic and conservation values).

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Data availability

Data analysed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors have declared no conflict of interest.

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Appendix A

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Fig. A1. The left panel projects the location of the study area in the southern portion of Argentina, identifying the distribution of sampling plots by blue dots ($n = 145$). *Nothofagus antarctica* forests are represented in orange, while *Nothofagus pumilio* and mixed evergreen forests are represented in green. Major cities are identified with squares. Map elaborated with resources provided by the National Geographic Institute (https://www.ign.gob.ar/; January 2023). The right panel shows the research approach indicating the natural dynamic phases and their relationships in *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (modified from Martínez Pastur et al. 2021). (i) Natural forests: IGP = initial growth phase, FGP = final growth phase (control 1), MAT = mature phase (control 2), DEC = decay phase, YUA = young uneven-aged, and MUA = mature uneven-aged. (ii) Harvesting: LH = low-intensity harvesting, HH = high-intensity harvesting, and CC = clear-cuts. (iii) Transformed and associated environments: FIRE = forests with fires, FER = forest edge regeneration, OPD = dry grasslands, and OPH = humid grasslands. Arrows indicate the expected evolution between phases.

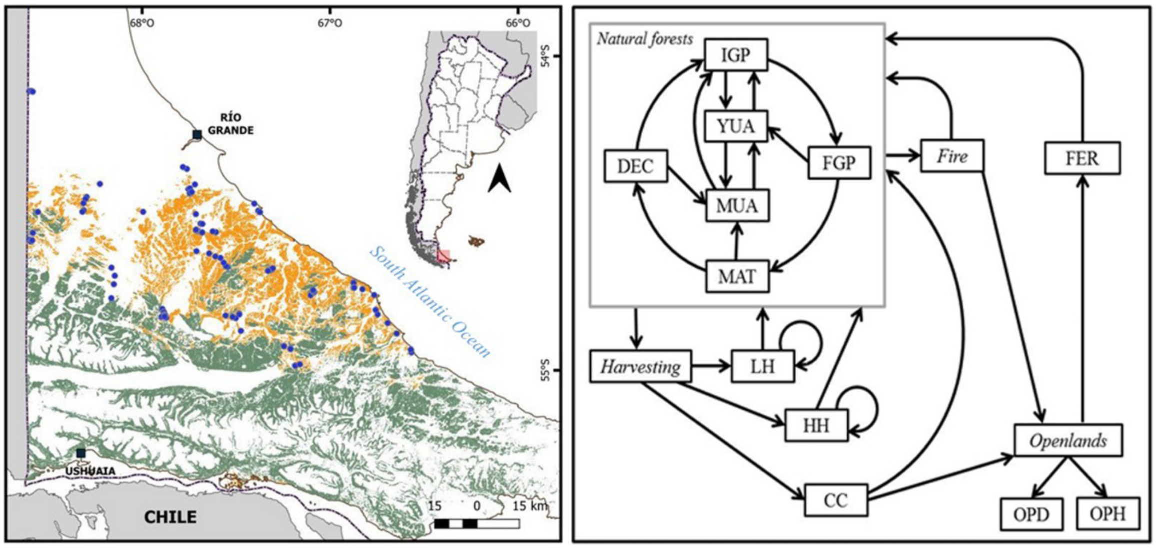

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Fig. A2. Contribution of each category to the total carbon storage (%) of the different forest treatments ((A) = natural cycle, (B) = harvesting, and (C) = transformed and associated environments) and forest phases (see Fig. A1) in *Nothofagus antarctica* forest landscapes (see Table 1). Categories are represented as trees = green, deadwood = gold, understory plants = red, and soil layer = brown. Within the bars are the net carbon stock values (t C ha^{-1}) of the main contributing categories. FGP and MAT were used as control treatments for comparisons.

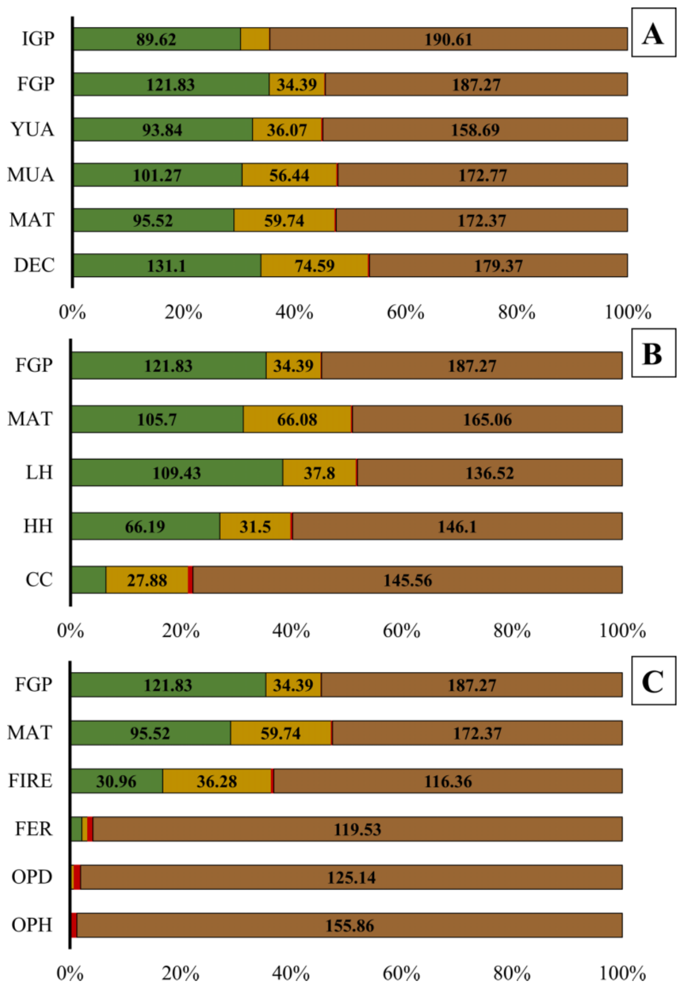

Table A1. Fisher's test (*F*) and probability (*p*) of ANOVAs analysing the total carbon storage (t C ha^{-1}) considering different forest treatments (natural cycle, harvesting, and transformed and associated environments) and forest phases (see Fig. A1) in *Nothofagus antarctica* forest landscapes, classified according to above- and belowground components (see Table 1). FGP and MAT were used as control treatments for comparisons. Outputs are presented in Fig. 1.

Factor	Levels	*F*(*p*)
Natural cycle	IGP	34.01(<0.01)
	FGP	409.48(<0.01)
	YUA	58.08 (<0.01)
	MUA	45.46(<0.01)
	MAT	227.20(<0.01)
	DEC	60.19(<0.01)
	Aboveground	1.82(0.13)
	Belowground	1.57(0.19)
Harvesting	FGP	409.48(<0.01)
	MAT	227.20(<0.01)
	LH	172.57(<0.01)
	HH	200.47(<0.01)
	CC	226.78(<0.01)
	Aboveground	15.26(<0.01)
	Belowground	14.17(<0.01)
Transformed and associated environments	FGP	409.48(<0.01)
	MAT	227.20(<0.01)
	FIRE	33.19(<0.01)
	FER	78.49(<0.01)
	OPD	230.59(<0.01)
	OPH	70.94(<0.01)
	Aboveground	39.91(<0.01)
	Belowground	16.04(<0.01)

Table A2. Importance of each carbon component (see Fig. A1) for the principal component analyses (PCA) considering different forest treatments (natural cycle, harvesting, and transformed and associated environments), analysing Axis 1 and Axis 2, where eigenvectors were scaled to the unit lengths.

	Natural cycle		Harvesting		Transformed and associated environments	
Component	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
LEA	0.3595	0.2497	−0.379	−0.1004	−0.3207	0.2158
BRA	0.4246	−0.1536	−0.3854	−0.0009	−0.337	0.1205
BAR	0.373	−0.2932	−0.3804	0.0668	−0.3391	0.056
WOO	0.3346	−0.3455	−0.3718	0.0973	−0.3369	0.0252
COR	0.4274	−0.1359	−0.3847	−0.0089	−0.3362	0.1279
FIR	−0.1198	−0.2108	0.0867	0.0132	−0.252	0.0123
CWD	0.0341	−0.2491	−0.0114	0.182	−0.2003	−0.3644
DET	−0.0664	−0.4113	−0.0833	0.6149	−0.1787	−0.5721
CRT	−0.0663	−0.4113	−0.0833	0.6149	−0.1787	−0.5721
WDS	−0.0354	−0.3291	−0.2766	0.0158	−0.3229	−0.0165
AUP	−0.2418	−0.1839	0.1656	0.2654	0.1731	−0.0485
DUP	−0.2081	−0.1976	0.1832	0.3184	0.0856	−0.2924
LIT	0.3597	0.2489	−0.3433	−0.072	−0.3206	0.2077
SOI	0.0081	0.0477	0.0051	0.0962	−0.1739	−0.0039

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Table A3. Multiresponse permutation procedure (MRPP) results comparing differences among groups of plots for carbon storage (t C ha^{-1}) considering different forest treatments (natural cycle, harvesting, and transformed and associated environments), where FGP and MAT were used as control treatments for comparisons. Acronyms are shown in Fig. A1. T = MRPP statistic, p = probability.

		Statistics	
Treatments	Group comparison	*T*	*p*
Natural cycle	Overall	−3.766	*0.001*
	IGP versus FGP	−0.979	*0.157*
	IGP versus YUA	−0.861	*0.171*
	IGP versus MUA	−1.973	*0.04*
	IGP versus MAT	−2.13	*0.037*
	IGP versus DEC	−3.774	*0.003*
	FGP versus YUA	−1.746	*0.062*
	FGP versus MUA	−1.702	*0.062*
	FGP versus MAT	−3.478	*0.006*
	FGP versus DEC	−4.261	*0.001*
	YUA versus MUA	−0.715	*0.212*
	YUA versus MAT	−0.717	*0.202*
	YUA versus DEC	−3.743	*0.006*
	MUA versus MAT	0.918	*0.856*
	MUA versus DEC	−1.181	*0.122*
	MAT versus DEC	−2.867	*0.014*
Harvesting	Overall	−22.633	*<0.001*
	FGP versus. MAT	−3.478	*0.006*
	FGP versus. LH	−7.882	*<0.001*
	FGP versus. HH	−11.67	*<0.001*
	FGP versus CC	−8.625	*<0.001*
	MAT versus LH	−7.462	*<0.001*
	MAT versus HH	−8.558	*<0.001*
	MAT versus CC	−10.871	*<0.001*
	LH versus HH	−19.874	*<0.001*
	LH versus CC	−19.084	*<0.001*
	HH versus. CC	−10.227	*<0.001*
Transformed and associated environments	Overall	−13.370	*<0.001*
	FGP versus MAT	−3.478	*0.006*
	FGP versus FIRE	−6.814	*<0.001*
	FGP versus FER	−9.932	*<0.001*
	FGP versus OPD	−7.021	*0.001*
	FGP versus OPH	−5.605	*0.002*
	MAT versus FIRE	−6.919	*<0.001*
	MAT versus FER	−13.94	*<0.001*
	MAT versus OPD	−10.660	*<0.001*
	MAT versus OPH	−8.043	*<0.001*
	FIRE versus FER	−4.664	*0.001*
	FIRE versus OPD	−5.588	*<0.001*
	FIRE versus OPH	−3.601	*0.006*
	FER versus OPD	−0.310	*0.318*
	FER versus OPH	−0.585	*0.222*
	OPD versus OPH	−1.216	*0.109*