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Changes in forest structure modify understory and livestock occurrence along the natural cycle and different management strategies in *Nothofagus antarctica* forests

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Abstract Sustainable forest management is proposed as a solution for many ecological and socio-economic trade-offs associated with different forest uses. In Patagonia, silvopastoral systems were proposed to balance provisioning ecosystem services and other natural values. However, the design of these practices needs a better understanding of livestock production. The objective of this study was to determine changes in the understory forage value and livestock occurrence in *Nothofagus antarctica* forests of Tierra del Fuego (Argentina) growing under a natural dynamic and in stands with impacts generated by harvesting, fires and silvopastoral uses. We sampled 145 areas determining forest structure, understory forage value (cover, biomass, forage quality) and livestock occurrence (wild and domestic stocking rate), including different forest conditions: (i) six phases of the natural forest cycle (even- and uneven-aged stands), (ii) four types of management and conversion alternatives (different thinning intensities, clear-cuts, and fires), and (iii) three associated environments (forest edges and grasslands). Main results showed that understory cover and biomass did not differ along the natural forest phases, but varied across management alternatives and associated environments. The magnitude of these changes was directly related to the impact degree. Forage quality did not change across the factors and levels. Livestock occurrence is related to the observed changes in the understory; however, a different behaviour was observed between wild and domestic herbivores. The different analyses highlighted the similarities in forage value and livestock occurrence among the different natural forest phases, and showed how the stands with different impacts differed from the control stands. The outputs could be used to improve forest management strategies in the framework of silvopastoral systems at landscape level.

Keywords Uneven-aged and even-aged forests · Understorey values · Stocking density · Forest resilience · Sustainable management · Patagonia

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Introduction

During Patagonia colonization (1850–1950), the first settlers clear-cut and fired forests for livestock farming (Gea et al. 2004). Recently, native forest landscape conservation has become an important social issue to preserve biodiversity and ecosystem services (ES) (Peri et al. 2021). Sustainable forest management is proposed as a solution for many ecological and socio-economic trade-offs associated with different forest uses (Perera et al. 2018). It aims to preserve ecosystem integrity together with wood and non-wood provisioning ES by maintaining forest structural complexity, species diversity, and ecological processes within the natural disturbance regimes. Silvopastoral systems was propose as an alternative to reach a balance between different ES (maximizing provisioning and minimizing trade-offs with other ES) and biodiversity (Martínez Pastur et al. 2017, 2021). In Patagonia, this proposal simplifies the natural structures of *Nothofagus antarctica* (ñire) forests by opening the canopy through thinning (Martínez Pastur et al. 2018), promoting understory development (Alonso et al., 2020), and in consequence, enhancing livestock production (Ormaechea and Peri 2015). This management increases provisioning ES (e.g. animal and timber production), decreases other ES (e.g. supporting or regulating), and modifies biodiversity and ecosystem functions (e.g. Soler et al. 2013; Martínez Pastur et al. 2021). The design of better sustainable productive practices in Patagonia needs a better understanding of impacts and drivers that influence livestock production, e.g. (i) changes in stocking rate due to different management proposals, (ii) livestock preferences of environments (natural or managed), (iii) understory changes (biomass and quality) due to management, and (iv) niche segregation between wild (e.g. *Lama guanicoe*, guanaco) and domestic herbivores (Martínez Pastur et al. 2016; Peri et al. 2016, 2017).

Plants vary in nutritive components that deliver to consumers. Nutritive values (e.g. protein, carbohydrate, fibre) influence herbivorous dietary requirements over time (Simpson et al. 2004; Lee 2018), e.g. wild and domestic herbivores have different forage requirements across the year in Patagonia (e.g. Soler et al. 2012). Besides, niche segregation exists among herbivorous species in forest landscapes (Iranzo et al. 2013; Schroeder et al. 2014), leading to overgrazing for displacements (e.g. guanaco tends to move to less productive environments). The nutritive components of plants can be characterized through different metrics, e.g. from dry matter content to digestibility (Beecher et al. 2015; Lee 2018). The understanding of this nutritive value improves the management strategies, e.g. forage species selection directed by wild herbivores (Delaby and Peyraud 2009). However, variation in nutritive value and palatability has not been comprehensively assessed (Lee 2018). Paddocks in Patagonia (100–1000 ha) usually contain mixed vegetation types (e.g. forests, grasslands, meadows). Therefore, animals select environments depending on forage quantity and quality, shelter or predator risks, e.g. Ormaechea and Peri (2015) reported that livestock prefers forests than openlands, associated with thermal conditions and forage.

Forest management must be clearly designed to maintain sustainability in the long-term, assuring the persistence capacity of ecosystems (Schröter et al. 2017). Silvopastoral systems provide several goods and services in Patagonia, however, the animal component has been little studied. The objective of this study was to determine changes in the understory forage value and livestock occurrence (wild and domestic) in ñire forests of Tierra del Fuego (Argentina) under a natural dynamic cycle and with different impact degrees (harvesting, fires, pastoral and silvopastoral uses). We intend to answer the following questions: (i) does understory forage value (cover, biomass, and forage quality) change across the different natural phases in even- and uneven-aged stands?, (ii) does understory forage value change across different harvesting intensities or in associated environments?, (iii) is livestock occurrence (wild or domestic) related to these changes?. In this work, we provide detailed information about nutritive value of understory in *N. antarctica* forests of Tierra del Fuego, analysing differences in forests under different natural dynamic phases and with a variation of artificial impacts, as well as a comparative estimation of current and potential wild and domestic herbivorous stocking rate. Finally, we discussing the trade-off between forage offer and demand, and their implications for conservation in the managed landscapes.

Materials and methods

Characterization of the sampling areas

This study was conducted in locations previously reported by Martínez Pastur et al. (2021), covering the natural distribution of ñire forests in Tierra del Fuego, Argentina (53°38′ to 54°37′ S, 66°28′ to 68°36′ W). The climate is cold oceanic with strong winds, mainly from the southwest. The mean annual temperature is 5.5 °C (1.6 °C in the coldest and 9.6 °C in the warmest months) and frost may occur at any time of the year. Precipitation is evenly spread over the year, with an annual average of 500 mm.yr^{-1} in the south coast of the island and about 1000 mm. yr^{-1} at the tree line, declining towards the north. The landscape occupied by forests is mostly that of glacial origin with loess and alluvial materials in the foothills. Acid brown soils are the most common (Gea et al. 2004). Sampling included 145 stands (even- and uneven-aged), and associated openlands (>2 ha each) including managed and unmanaged landscapes. The design (Fig. 1) included six phases of the natural life-cycle (Ivancich 2013): (i) initial growth phase (IGP) (20–40 years-old) (n = 4 stands), (ii) final growth phase (FGP) (40–80 years-old) (n = 6 stands), (iii) mature phase (MAT) (80–120 years-old) (n = 12 stands), and (iv) decay phase (DEC) (120 to ~ 220 years-old) (n = 5 stands). The uneven-aged stands included: (v) young uneven-aged (YUA) when IGP or FGP are the main growth phases (n = 11 stands), and (vi) mature uneven-aged (MUA) when MAT and DEC are dominant (n = 9 stands). For the different analyses, we selected two controls for the comparisons: (i) MAT forests because is the climax stage and represent one of the conservation target at this latitudes (Martínez Pastur et al. 2020), and FGP because is the preferred structure for thinning, due to the closeness of the forest canopy that impede the understory plant growth.

Harvested stands were classified according to cut intensity (Fig. 1): (vii) low intensity harvesting (LH) with basal area (BA) > 30 m^2 ha^{-1} (n = 27 stands), (viii) high intensity harvesting (HH) with BA 5–30 m^2 ha^{-1} (n = 31 stands), and (viii) clear-cuts when BA < 5 m^2 ha^{-1} (n = 9 stands). (ix) Intentional fires were implemented (FIRE) (n = 8 areas) to remove trees and deadwood from the stands and convert the lands in pastures or natural grasslands to promote forage production for livestock. Finally, we included the associated environments: (x) forest edges where forests advance over openlands (FER) (n = 13 areas), (xi) grasslands dominated by *Festuca gracillima* and *Empetrum rubrum* (OPD) (n = 6 areas), and (xii) wetlands (OPH) dominated by *Juncus scheuchzerioides*, *Carex curta*, *C. macrosolen* and *Caltha sagittata* (n = 4 areas). See detailed descriptions in Martínez Pastur et al. (2020, 2021).

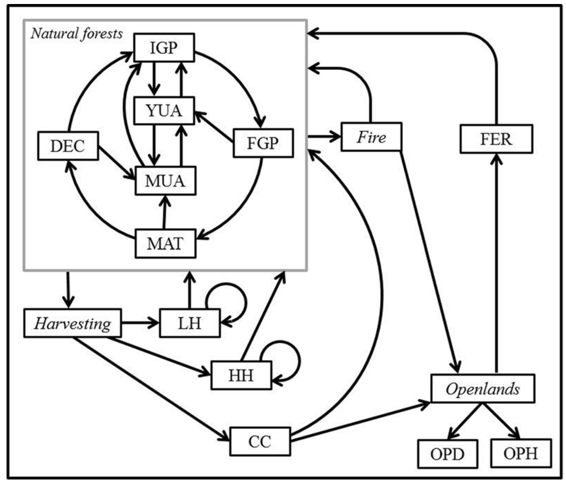

Fig. 1 Research approach indicating the natural dynamic phases and their relationships in the *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (Argentina) (modified from Martínez Pastur et al. 2021): (i) Natural dynamic forests: *IGP* initial growth phase, *FGP* final growth phase, *MAT* mature phase (control), *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) Associated environments: *FIRE* Forests with fires, *OPD* dry grasslands, *OPH* humid grasslands, and *FER* forest edge regeneration. Arrows indicate the expected evolution between phases

Characterization of the vegetation

We placed a 50 m transect in each stand to characterize the understory. We used point-intercept method (Levy and Madden 1933) with 50 intercept points every 1 m, recording vascular plants (dicots, monocots, ferns) and tree regeneration (< 1.30 m height), bare soil, litter, and woody debris to calculate ground cover. Plants were identified and classified according to their palatability for livestock using literature and stakeholder's expertise (Correa 1969–1998; Moore 1983). We collected above-ground biomass in 0.25 m^2

subplots associated with each transect during middle summer (January), which was dried in oven at 70 °C until constant weight and manually sorted in: (i) dead or alive, (ii) dicots, monocots, mosses and ferns, and (iii) palatable or unpalatable. We determined: understory cover (UC, %), palatable plant cover (PPC, %), unpalatable plant cover (UPC, %), understory plant dry biomass (UB, kg ha^{-1}), understory alive plant dry biomass (UAB, kg ha^{-1}), understory dead plant dry biomass (UDB, kg ha^{-1}), palatable UAB (UPB, kg ha^{-1}), dicot UPB (DUPB, kg ha^{-1}), monocot UPB (MUPB, kg ha^{-1}), and ratio between UPB and UB (RATIO, %).

Forage quality

Composite dried samples by plot, sorted by palatable and unpalatable plants, were grounded using a Wiley-Mill grinder with 1-mm sieve. The forage quality was measured as the digestibility of dry matter. Acid detergent fibre (ADF) and neutral detergent fibre (NDF) concentrations were determined using Ankom 2000 Fibre Analyser filter bag technique (Ankom Technology, USA) following a modification of Van Soest et al. (1991). ADF represents the material remaining after boiling in acid detergent (lignin, cellulose, silica, and insoluble nitrogenous compounds). NDF represents the material remaining after boiling in neutral detergent (lignin, silica, cellulose, and hemicellulose). Lignin was included as acid detergent lignin (ADL), which was isolated by boiling in acid (Lee 2018). Finally, mineral ash values were obtained after burning at 500 °C for 24-h. We obtained the percentage of hemicellulose, cellulose, lignin, mineral ash, and cell contents, calculating: (i) Dry matter digestibility (DMD, %) according to Linn and Martin (1989), where $DMD(\%) = 88.9 - (0.779 \times ADF(\%))$; (ii) Neutral detergent fibre (NDF, %) as the sum of cellulose, lignin, and mineral ash; (iii) The metabolizable energy content (MEC, Mcal), calculated as $MEC(Mcal) = 3.61 \times DMD(\%)$ (Menke and Steingass 1988); (iv) Crude protein content (CPC, %), calculated through total nitrogen content by Kjeldahl and multiplied by 6.25 (Mariotti et al. 2008). Finally, we developed one integrative forage quality index (Q, where 1 is high and 5 is low) based on the following thresholds: DMD ($>70\%$ is high, $<50\%$ is low), NDF ($<50\%$ is high, $>65\%$ is low), and CPC ($>15\%$ is high, $<8\%$ is low). We calculated these metrics for palatable alive plants (PDMD, PNDF, PMEC, PCPC, and PQ), and total alive plants (TDMD, TNDF, TMEC, TCPC, and TQ).

Livestock occurrence

We recorded animal feces from native (guanaco) and domestic animals (cows, sheep, horses) along each transect (200 m^2). Guanacos are free-ranging animals and moving across the landscape according their food and shelter requirements (Martínez Pastur et al. 2016), while domestic animals live in paddocks and are moved by ranchers according management objectives. We used this as a proxy of livestock occurrence ($animal.ha^{-1}$) assuming: (i) Feces was maintained in the floor for one calendar year (decomposition rate was low during summer due to low temperatures and high during winter due to mechanical effects of snow accumulation) (Bahamonde et al. 2017). (ii) Average defecation per day were defined as 12.3 times per day for cows and horses, and 6.0 times per day for sheep and guanacos. (iii) Requirements of dry matter forage (palatable plants) vary according to the animals (325 kg $DM.yr^{-1}$ for sheep, 650 kg $DM.yr^{-1}$ for guanacos, and 3250 kg $DM.yr^{-1}$ for cows and horses). In addition, we considered different residual palatable biomass for calculations of stocking rate (130 kg DM ha^{-1} for sheep and guanacos, and 260 kg $DM.ha^{-1}$ for cows and horses). Finally, (iv) we use sheep equivalent (SE) based on the animal species size (0.50 for guanaco, 0.16 for cows, and 0.10 for horses) to standardize values. With these data we determined: guanacos stocking rate (LG, SE ha^{-1}), livestock stocking rate (cattle, sheep, horses) (LIV, SE ha^{-1}), total stocking density (guanacos and livestock) (TSD, SE ha^{-1}), potential stocking rate based on food availability (POT, SE ha^{-1}), and grazing pressure (TSD-POT) (GP, SE ha^{-1}).

Statistical analyses

We defined three factors with several levels: (i) natural dynamic cycle (IGP, FGP, YUA, MUA, MAT, DEC), (ii) harvesting intensity (LH, HH, CC) and controls (FGP, MAT), (iii) associated environments (FIRE, FER, OPD, OPH) and controls (FGP, MAT). We used one-way ANOVA to test the differences, using Fisher and Tukey tests at $p<0.05$. We analyzed the following variables: (i) livestock occurrence (LG, LIV, TSD, POT, GP), (ii) vegetation cover and biomass (UC, PPC, UPC, UB, UAB, UDB, UPB, DUPB, MUPB, RATIO), and (iii) forage quality (PDMD, PNDF, PMEC, PCPC, PQ, TDMD, TNDF, TMEC, TCPC, TQ). Data were also characterized using three indexes to compare livestock occurrence, following Martínez Pastur et al. (2021). The values were standardized between 0 and 1, and each index was defined as the average value of each set of variables: (i) forest structure index (FI) previously calculated by Martínez Pastur et al. (2021), that includes crown cover, height, vigour, tree diameter, basal area, volume, and growth; (ii) livestock occurrence index (AI) (LG, LIV, TSD, POT, GP); and (iii) vegetation index (VI) (UC, PPC, UPC, UB, UAB, UDB, UPB, DUPB, MUPB, RATIO, PDMD, PNDF, PMEC, PCPC, PQ, TDMD, TNDF, TMEC, TCPC, TQ). The standard error of indexes was calculated for further comparisons. To evaluate multivariable influence on plots, we performed Principal Component Analysis (PCA), comparing separately the three studied factors and levels: (i) natural dynamic cycle, (ii) harvesting intensity compared to controls (FPG and MAT), and (iii) fires and associated environments compared to controls (FPG and MAT). In each PCA, we analyzed the whole group of variables (10 of vegetation cover and biomass, 10 of forage quality, and 5 of livestock occurrence), but only those with low redundancy and higher correlation were selected to representation (eigenvalues > 0.200 in the two first axis). These analyses graphically display similarities among plots according to the evaluated characteristics (vegetation cover and biomass, forage quality, livestock occurrence), reducing the dimensionality of multivariate data whilst minimizing loss of information, and allowing to detect the more relevant characteristics to represent variability (Pearson 1901; Jolliffe 2002; Jolliffe and Cadima 2016). PCA was complemented with a Monte Carlo permutation test ($n = 999$) to assess the significance of each axis. We selected correlation coefficients among columns to obtain the final cross-product matrices. We used PCORD 5.0 software (McCune and Mefford 1999).

Results

Changes in the vegetation cover and biomass

Vegetation cover and biomass did not significantly vary among levels across the natural cycle (Table 1). Young structures (IGP and FGP) presented lower values compared to uneven-aged and mature stands, but these differences were not significant. Harvesting significantly increased many of the studied variables (Table 1), which changed according to the cut intensity. In example, understory (total, alive, dead) and palatable (total, monocots) biomass significantly increased in the most intensive harvesting (CC) compared to young control (FGP), but some of these differences were not significant compared to mature control (MAT). Besides, MAT did not present significant differences with low and medium intensity harvesting (LH and HH). Associated environments presented significant differences in some variables due to fires (FIRE), or in natural grasslands (OPD and OPH), and forest edges (FER) (Table 1). FIRE only differed in palatable biomass (UPB) compared with MAT. FER had the same response as FIRE but also differed from young control (FGP) in the ratio between palatable and total biomass (RATIO) presenting the lowest values. Palatable plants (UPB and MUPB) in dry grasslands (OPD) did not differ from MAT but showed higher values than young control (FGP) in the palatable plants (UPB and MUPB). Finally, the most humid openlands (OPH) showed the greater differences among the studied levels, being significantly higher than both controls for palatable (UPB and MUPB) and unpalatable plant covers (UPC) due to the presence of dwarf shrubs (e.g. *Empetrum rubrum*) (data not shown), and also differed from young control (FGP) in total over (UC).

Forage quality (dry matter digestibility, metabolizable energy content, crude protein, and one quality index) of total and palatable plants did not significantly vary for the studied factors (natural cycle, harvesting, associated environments) when levels and controls were compared (Table 2). Beside the lack in significant differences, the higher quality forage according the developed index (PQ and TQ) were: (i) In the natural cycle, greater PQ was found in uneven-aged mature stands (MUA) and lower in decaying stands (DEC), while the best TQ occurred in young stands (IGP and FGP) and worst in older

Table 1 ANOVAs for the different factors and levels characterizing understory vegetation cover and biomass measured in *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (Argentina)

Factor	Levels	UC (%)	PPC (%)	UPC (%)	UB (kg ha^{-1})	UAB (kg ha^{-1})	UDB (kg ha^{-1})	UPB (kg ha^{-1})	DUPB (kg ha^{-1})	MUPB (kg ha^{-1})	RATIO (%)
Natural cycle	IGP	124.8	96.6	28.1	541.6	396.7	144.9	246.2	163.8	82.4	58.20
	FGP	146.0	120.7	25.3	845.9	643.5	202.4	578.5	331.2	247.3	69.75
	YUA	169.8	132.7	37.1	1609.1	882.5	726.6	736.9	131.5	605.4	46.98
	MUA	174.9	138.3	36.7	1828.7	1033.2	795.5	894.0	286.0	608.0	52.16
	MAT	172.1	145.2	26.9	1855.6	1052.3	803.3	1001.3	342.4	658.9	56.38
	DEC	202.3	171.7	30.6	1974.1	1140.8	833.3	1117.2	322.6	794.6	56.40
	F(p)	*0.87(0.510)*	*0.94(0.466)*	*0.43(0.822)*	*1.35(0.263)*	*0.77(0.574)*	*1.96(0.106)*	*1.26(0.299)*	*1.02(0.418)*	*1.26(0.302)*	*1.68(0.160)*
Harvesting	FGP	146.0	120.7	25.3	845.9a	643.5a	202.4a	578.5a	331.2	247.3a	69.8
	MAT	172.1	145.2	26.9	1855.6b	1052.3a	803.3ab	1001.3ab	342.4	658.9a	56.4
	LH	172.6	147.9	24.7	1455.7b	881.7a	574.0a	815.6a	279.3	536.2a	58.2
	HH	175.6	145.8	29.8	2130.1b	1392.3ab	737.8a	1189.7ab	426.0	763.7a	52.7
	CC	186.3	152.2	34.1	3752.2c	2418.0b	1334.2b	1982.8b	322.1	1660.7b	49.0
	F(p)	*0.43(0.785)*	*0.35(0.846)*	*0.52(0.725)*	*5.57(<0.001)*	*4.50(0.002)*	*5.83(<0.001)*	*2.89(0.027)*	*0.32(0.866)*	*4.46(0.003)*	*2.23(0.072)*
Associated environments	FGP	146.0a	120.7ab	25.3a	845.9	643.5	202.4	578.5a	331.2	247.3a	69.8b
	MAT	172.1ab	145.2ab	26.9a	1855.6	1052.3	803.3	1001.3b	342.4	658.9ab	56.4ab
	FIRE	148.4a	115.2ab	33.3ab	2049.2	1297.1	752.1	763.2a	393.9	369.4a	38.3ab
	FER	129.9a	63.6a	66.3ab	3164.2	2541.5	622.6	354.9a	104.4	250.5a	22.0a
	OPD	131.1a	75.6a	55.5ab	3494.6	2501.2	993.4	1082.0b	4.5	1077.5b	46.4ab
	OPH	251.5b	168.3b	83.3b	3273.1	2283.5	989.6	2283.5c	506.7	1776.8c	71.6b
	F(p)	*3.31(0.014)*	*3.43(0.012)*	*6.78(<0.001)*	*2.38(0.058)*	*2.46(0.052)*	*2.42(0.055)*	*8.57(<0.001)*	*1.71(0.159)*	*16.6(<0.001)*	*5.47(<0.001)*

F Fisher test, *p* probability at $p<0.05$. Acronyms for the different levels were explained in Fig. 1

UC understory cover (%), *PPC* palatable plant cover (%), *UPC* unpalatable plant cover (%), *UB* understory plant dry biomass (kg ha^{-1}), *UAB* understory alive plant dry biomass (kg ha^{-1}), *UDB* = understory dead plant dry biomass (kg ha^{-1}), *UPB* palatable UAB (kg ha^{-1}), *DUPB* dicot UPB (kg ha^{-1}), *MUPB* monocot UPB (kg ha^{-1}), and *RATIO* ratio between UPB and UB (%)

Table 2 ANOVAs for the different factors and levels characterizing forage quality of understory plants measured in *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (Argentina)

Factor	Levels	PDMD (%)	PNDF (%)	PMEC (Mcal)	PCPC (%)	PQ	TDMD (%)	TNDF (%)	TMEC (Mcal)	TCPC (%)	TQ
Natural cycle	IGP	66.7	28.5	2.41	9.0	3.0	62.0	34.6	2.24	8.3	3.3
	FGP	66.1	29.3	2.39	9.2	3.2	63.8	32.3	2.30	8.7	3.3
	YUA	66.9	28.3	2.41	8.8	3.3	62.7	33.6	2.26	7.3	3.7
	MUA	67.1	28.0	2.42	10.4	2.8	62.8	33.5	2.27	8.4	3.7
	MAT	67.9	27.0	2.45	8.8	3.0	64.0	32.0	2.31	7.6	3.8
	DEC	65.8	29.7	2.37	7.7	3.6	62.8	33.5	2.27	6.6	3.8
	F(p)	*0.29(0.914)*	*0.29(0.914)*	*0.29(0.914)*	*0.62(0.683)*	*0.70(0.629)*	*0.54(0.748)*	*0.54(0.748)*	*0.54(0.748)*	*1.04(0.408)*	*1.11(0.368)*
Harvesting	FGP	66.1	29.3	2.39	9.2	3.2	63.8	32.3	2.30	8.7	3.3
	MAT	67.9	27.0	2.45	8.8	3.0	64.0	32.0	2.31	7.6	3.8
	LH	67.1	27.9	2.42	9.3	3.0	63.6	32.5	2.29	8.2	3.4
	HH	67.7	27.2	2.44	9.1	3.1	63.9	32.1	2.31	8.0	3.5
	CC	65.5	30.0	2.36	7.9	3.6	62.8	33.5	2.27	7.3	3.8
	F(p)	*0.81(0.521)*	*0.81(0.521)*	*0.81(0.521)*	*0.88(0.479)*	*1.07(0.375)*	*0.30(0.876)*	*0.30(0.876)*	*0.30(0.876)*	*1.52(0.204)*	*1.42(0.234)*
Associated environments	FGP	66.1	29.3	2.39	9.2	3.2	63.8	32.3	2.30	8.7	3.3
	MAT	67.9	27.0	2.45	8.8	3.0	64.0	32.0	2.31	7.6	3.8
	FIRE	70.0	24.2	2.53	9.8	2.8	64.7	31.1	2.34	7.7	3.6
	FER	66.8	28.3	2.41	8.4	3.6	59.6	37.6	2.15	6.6	3.8
	OPD	66.9	28.2	2.42	7.8	3.5	62.3	34.1	2.25	6.6	4.0
	OPH	65.5	30.1	2.36	7.1	4.0	62.3	34.1	2.25	6.2	4.0
	F(p)	*1.17(0.344)*	*1.17(0.344)*	*1.17(0.344)*	*1.34(0.272)*	*1.82(0.134)*	*1.69(0.163)*	*1.69(0.163)*	*1.69(0.163)*	*1.90(0.119)*	*2.00(0.102)*

F Fisher test, *p* probability at $p<0.05$. Acronyms for the different levels were explained in Fig. 1

PDMD dry matter digestibility of palatable alive plants (%), *PNDF* neutral detergent fibre of palatable alive plants (%), *PMEC* metabolizable energy content of palatable alive plants (Mcal), *PCPC* crude protein content of palatable alive plants (%), *PQ* quality index of palatable alive plants (1 is high to 5 is low 1 to 5), *TDMD* dry matter digestibility of total alive understory plants (%), *TNDF* neutral detergent fibre of total alive understory plants (%), *TMEC* metabolizable energy content of total alive understory plants (Mcal), TCPC crude protein content of total alive understory plants (%), and TQ = quality index of total alive understory plants (1 is high to 5 is low) stands (MAT and DEC). (ii) In the harvesting, the best PQ was found in mature and light-harvesting stands (MAT and LH) and the worst in clear-cuts (CC), while the best TQ was found in the young control (FGP) and the worst in mature stands (MAT) and clear-cuts (CC). And (iii) in associated environments, PQ was higher in burned areas (FIRE) and the worst in the humid grasslands (OPH), while the best total plant index (TQ) was found in the young control (FGP) and the worst in nature grasslands (OPD and OPH).

Changes in the livestock occurrence

Livestock occurrence did not significantly varied across the natural cycle (Table 3). Despite the lack of significant differences, we can observe a higher guanaco use in the uneven-aged forests (YUA and MUA) compared to other levels; however, livestock was higher in older stands (MAT and DEC) and lower in the young ones (IGP and FGP). Guanaco represents 4.3% of the total stocking density, being higher (7.4%) in the young stands (IGP) and lower (0.7%) in the older stands (MAT and DEC). Surprisingly, the grazing pressure showed negative values in most of the levels evidencing an undergrazed situation, except for DEC.

Livestock occurrence significantly varied with harvesting (Table 3) for guanaco use (LG) and the potential stocking rate (POT), where clear-cuts differed from both controls. Despite the lack of significant differences, we observed more livestock use in clear-cuts and mature control (MAT) than in other levels. Guanaco represents 11.3% of the total stocking density in the harvested stands (LH, HH, CC), being higher (22.4%) in the clear-cuts (CC) than in harvested areas (5.7% in LH and HH). Finally, there were negative values of grazing pressure for all the

Table 3 ANOVAs for the different factors and levels characterizing livestock occurrence measured in *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (Argentina)

Factor	Levels	LG (SE ha^{-1})	LIV (SE ha^{-1})	TSD (SE ha^{-1})	POT (SE ha^{-1})	GP (SE ha^{-1})
Natural cycle	IGP	0.02	0.25	0.27	0.36	-0.08
	FGP	0.02	0.28	0.30	1.42	-1.11
	YUA	0.11	1.55	1.66	1.88	-0.21
	MUA	0.05	1.26	1.31	2.35	-1.04
	MAT	0.02	2.53	2.55	2.68	-0.13
	DEC	0.02	3.17	3.19	3.04	0.15
	F(p)	*1.02(0.416)*	*0.68(0.644)*	*0.67(0.645)*	*1.25(0.303)*	*0.11(0.989)*
Harvesting	FGP	0.02a	0.28	0.30	1.42a	-1.11
	MAT	0.02a	2.53	2.55	2.68ab	-0.13
	LH	0.10ab	1.06	1.16	2.11ab	-0.95
	HH	0.05ab	1.74	1.78	3.26ab	-1.48
	CC	0.66b	2.28	2.94	5.70b	-2.76
	F(p)	*2.48(0.049)*	*1.48(0.215)*	*1.60(0.183)*	*2.87(0.028)*	*0.55(0.697)*
Associated environments	FGP	0.02	0.28	0.30	1.42a	-1.11ab
	MAT	0.02	2.53	2.55	2.68a	-0.13ab
	FIRE	0.06	1.79	1.86	1.97a	-0.11ab
	FER	0.01	3.22	3.23	0.75a	2.48b
	OPD	0.03	3.15	3.18	2.93a	0.26ab
	OPH	0.00	2.28	2.28	6.63b	-4.35a
	F(p)	*0.60(0.699)*	*0.98(0.443)*	*0.97(0.448)*	*8.62(<0.001)*	*2.80(0.031)*

F Fisher test, *p* probability at $p < 0.05$. Acronyms for the different levels were explained in Fig. 1

LG Lama guanicoe expressed in sheep equivalents (SE) per hectare, *LIV* livestock (cattle, sheep, horses) (SE ha^{-1}), *TSD* total stocking density (*L. guanicoe* and livestock) (SE ha^{-1}), *POT* potential stocking density based on food availability (SE ha^{-1}), and *GP* = grazing pressure (TSD – POT) (SE ha^{-1})

studied levels. Livestock occurrence significantly varied when we compared associated environments (Table 3) for potential stocking rate (POT) and the grazing pressure (GP). Humid grasslands (OPH) had significantly greater food availability than other levels, where the minimum was observed in the edges (FER). Guanaco use was related to livestock (e.g. was greater when livestock was minimum), but on average was very low (1.3%) compared to livestock (98.7%). Finally, we observed significant differences in grazing pressure, with high overgrazing in FER, moderate grazing in OPD, and a remarkable undergrazing in OPH.

Relation between stocking rate and forage availability

When indexes were contrasted (Fig. 2), we found that factors and levels were split in groups: (i) The forest structure (FI) and vegetation (VI) indexes showed that natural cycle phases had similar values, also comparable to low-intensity harvesting (LH). Values of FI decreased and VI increased according to the impact (HH > FIRE > CC in FI), which were more similar to values of openlands (FER < OPD < OPH in VI). (ii) The comparison between FI and animal index (AI) followed a similar pattern, indicating that thinning intensity (LH and HH) had similar stocking rate despite the forest structure. Finally, (iii) the

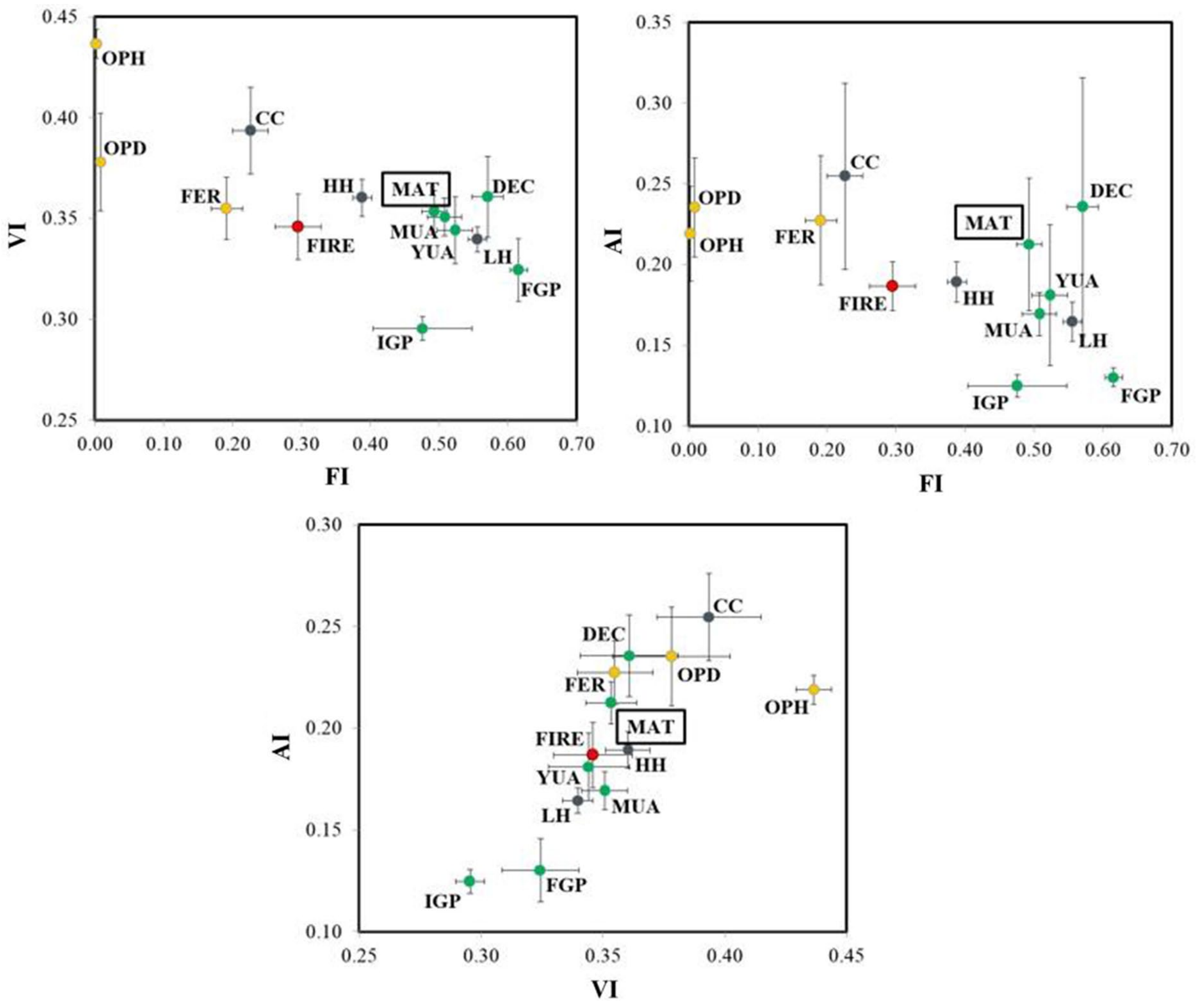

Fig. 2 Relation among groups of variables for the different natural dynamic phases (see acronyms in Fig. 1) of *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (Argentina). *FI* forest structure index, *VI* vegetation index, and *AI* animal index. Bars indicate standard error for each axis

comparison between VI and AI showed a different pattern, indicating that forest structure and forage availability are not totally related as we described before. Young stands (IGP and FGP) were similar, with the lowest VI and AI values. Other conditions, including uneven-aged stands, low and medium intensity harvesting (LH and HH), and fires (FIRE), showed intermediate values of both indexes, while mixed older stands (MAT and DEC), some openlands (FER and OPD), and clear-cuts (CC), had similar VI but higher AI. Finally, the OPH occupied the most distant area of the graph (with high values for both indexes).

The plots corresponding to the natural dynamic phases were mixed in the PCA (Fig. 3A), although young stands (IGP and FGP) conformed a more

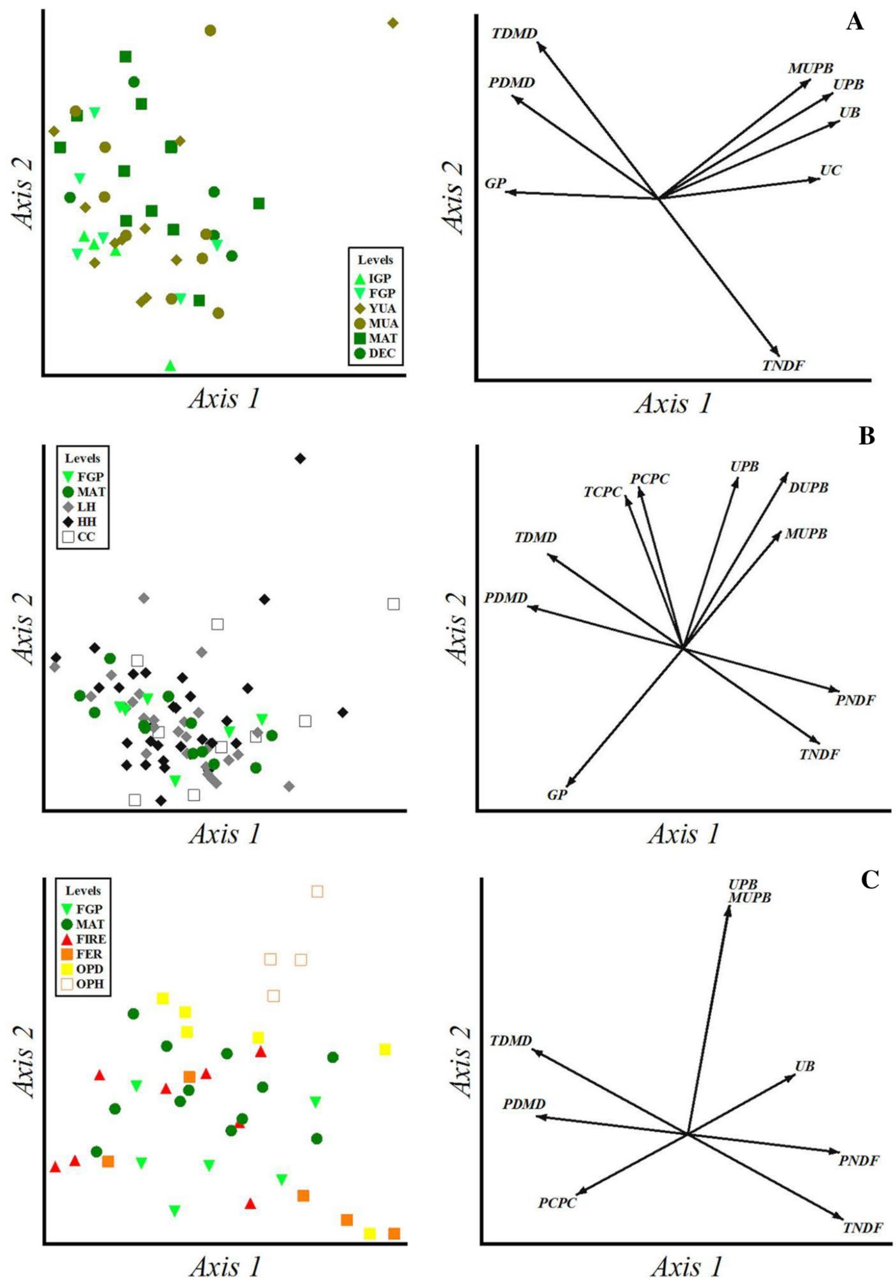

Fig. 3 PCA considering the natural dynamics phases **A**, the harvesting **B**, and forests affected by fire also with open-lands in forested landscapes **C** of *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (Argentina) (see acronyms in Fig. 1 for levels, and in Tables 1, 2, 3 for variables)

conspicuous group with less dispersion than mature or uneven-aged stands. Eigenvalues for the first two components (Fig. 3A) were 4.160 ($p < 0.001$) and 2.300 ($p < 0.001$) respectively, explaining 52.0% and 80.8% of the cumulative variance. The variables more correlated with Axis 1 were UB > UPB > UC > GP, while for Axis 2 were TDMD > TNDF > MUPB > UPB. PCA for harvesting (Fig. 3B) presented less separation of groups. Eigenvalues for the first two components (Fig. 3B) were 4.335 ($p < 0.001$) and 2.592 ($p < 0.001$), explaining 43.3% and 69.3% of the cumulative variance. The variables more correlated with Axis 1 were PDMD > PNDF > TDMD > TNDF, while for Axis 2 were UPB > DUPB > TCPC > PCPC. Finally, PCA for associated environments (Fig. 3C), showed a very clear separation between FIRE and openlands, with OPH as the more conspicuous group. Eigenvalues for the first two components (Fig. 3C) were 4.120 ($p < 0.001$) and 2.057 ($p < 0.001$), explaining 51.5% and 77.2% of the cumulative variance. The variables more correlated with Axis 1 were TDMD > TNDF > PNDF > PDMD, while those for Axis 2 were UPB > MUPB.

Discussion

At higher latitudes, natural forests show simple horizontal and vertical structures, usually with one dominant species and one or two overstory strata, following predictable forest dynamic paths (Martínez Pastur et al. 2021). Ñire forests mainly grow in the ecotone areas between forests and steppe, where ranching prevails (Ormaechea and Peri 2015). These forests present more richness and biomass of understory and less timber values compared to other *Nothofagus* forests, and for this, silvopastoral management was proposed (Peri et al. 2016). The thinning opens the canopy and promotes understory growth and timber quality of trees (Martínez Pastur et al. 2018), generating positive synergies with nutrient and water cycles (Gargaglione et al. 2014). Besides, forests offer shelter for animals during night, winter, and frequent storms (Ormaechea and Peri 2015). Our results highlight the advantages of silvopastoral management (e.g. LH and HH) compared to land transformation (in this paper represented by FIRE and CC), in terms of forage availability/quality and livestock occurrence. Besides, the comparison of these managements with other associated environments is needed because most managers only consider grasslands areas (OPD and OPH) to adjust livestock stocking rate in paddocks.

The forest interventions usually increase understory biomass and cover, as well as forage quality (Peri et al. 2016; Ford et al. 2019). The feeding value of forage is defined as the animal production response to the total forage consumed, as function of voluntary intake, digestibility, and efficiency of use of absorbed nutrients. Here, the forage quantity and quality did not significantly vary in natural forests (Tables 1 and 2), although other studies stated that differences can be detected at micro-site level (e.g. below or between canopy trees) according to natural heterogeneity of the managed stands (Gargaglione et al. 2014; Sanna et al. 2021). Thinning opens the canopy allowing understory growth by increasing monocots and maintaining dicot species (Mosquera-Losada et al. 2018; Schmiedgen et al. 2021). Our results support this, as the main advantage of silvopastoral systems, which preserve the understory diversity with the associated positive synergies, e.g. dicot plants offer higher dietary quality (e.g. protein content) compared to monocots (Bumb et al. 2016; Srivastava and Kumar 2021). Besides, our study showed that some associated environments presented less cover of palatable species (e.g. OPD and FER) compared to unmanaged natural forests, but similar palatable biomass with few species (e.g. OPD were mainly *Festuca gracillima*) (Oliva et al. 2005). Other associated environments were not studied here, as wetlands (e.g. close to rivers) occupy a small percentage of the landscape (< 5%) but had the highest cover and palatable biomass (Enriquez et al. 2015). Despite this, we did not find differences in forage quality across the studied environmental gradient (Table 2). Although some species presented higher quality than others (Lee 2018), we evaluated forage quality without discriminating species, which could explain the lack of differences. However, quality indexes (Table 2) showed better values in low-intensity managed forests (LH and HH) compared to clear-cuts; and in forests compared to openlands. An increase of annual understory crude protein concentration in ñire forests under silvopastoral management from 9.9 to 11.2%, was also reported by Peri et al. (2016). Also, those authors found a monthly variation in understory organic matter digestibility, ranged from 43.7 to 78.5% depending on the time during the growing season, and light intensity.

Natural fires do not occur in the Fuegian archipelago, and ñire forests are not adapted to these impacts (Peri et al. 2017; Martínez Pastur et al. 2021). Intentional fires were used as land conversion practice in Patagonia (Gea et al. 2004), to remove forests and transform to grasslands, currently considered more appropriate for livestock production (Huber and Markgraf 2003). Fires generate large modifications in the transformed ecosystems leading to different vegetation dynamic pathways (Veblen et al. 1992; Armesto et al. 1992). With time, these burned areas were converted to artificial grasslands (Bahamonde et al. 2012), allowing the invasion of species that decrease the forage potential (e.g. *Hieracium pilosella*) (Alonso et al. 2020; Martínez Pastur et al. 2020). In our study, instead, fires did not improve the forage cover and biomass (Table 1), while quality index slightly increased.

Forage availability is the main driver for livestock occurrence, but also distance to water, animal welfare, accessibility, predation risks, shelter against extreme climate, and soil conditions (e.g. excess of humidity) are important drivers (Ormaechea and Peri 2015; Macedo Pezzopane et al. 2019; Sánchez-Romero et al. 2021). In this work, we provide evidences about another influential factor, as the trade-offs with natural populations of native herbivores (guanacos), which compete for forage across seasons (e.g. Soler et al. 2012). This competition generates niche segregation (Iranzo et al. 2013; Schroeder et al. 2014), driving guanacos to use the resting paddocks or marginal environments. In our study, guanacos and livestock density did not greatly change across natural forests, being higher in open forests (e.g. mature open uneven-aged stands > young closed even-aged stands). Contrary to our expectations, harvesting was not associated to significantly different livestock stocking density, even when forage availability was greater in harvested stands. The presence of over/undergrazed areas in the same paddock could influence this lack of differences in the stocking rate. Ormaechea and Peri (2015) indicate that paddock size (300–500 ha) is the main reasons for undergrazing of some areas, due to distance to water or preference for openlands. However, guanacos significantly increased according food availability, showing better adaptation to environmental changes (Soler et al. 2013; Martínez Pastur et al. 2016). This was consistent with the overgrazing detected in FER and OPD, where animals selected areas close to forests for feeding (e.g. feeding in the openlands during the day and look for shelter during the night) (Ormaechea and Peri 2015).

The relation among the studied variables and the different natural dynamic phases (Fig. 2) showed that harvesting generates different pathways for understory development and livestock occurrence, depending on the harvesting intensity. Forest management creates a wide range of modifications, from small (e.g. selective cuttings) to very high impacts (e.g. grasslands generated by clear-cuts or heavy fires) (Gea et al. 2004; Martínez Pastur et al. 2021). The magnitude of these changes was directly related to the cut intensity. Human activities affect the ES provision, but also forest resilience, which can lead to permanent modifications in structure and functions (Peri et al. 2017). Stand modifications can lead to positive synergies (e.g. increase livestock stocking density) but also, to trade-offs with other ES or loss of resilience to natural impacts (e.g. insect outbreaks or climate change) (Martínez Pastur et al. 2018). Therefore, it would be desirable to maintain the natural values of managed stands (e. g. conservation reserves within the managed areas, as "land-sharing") instead to promote the creation of hybrid or novel ecosystems (Evers et al. 2018), as often occurs with clear-cuts and fires, but also with high intensity harvesting practices. Understanding the variation in forage production and quality of stands under natural dynamics associated with natural and anthropic disturbances, as well as the comparison between current and potential wild and domestic herbivorous stocking rate, provides information about trade-offs between forage offer and demand and forest resilience, which should be considered in proposals for sustainable management in the long-term.

Conclusions

Understory biomass and quality do not greatly change across the different phases of the natural dynamic cycle in the ñire forests, which were under the influence of different natural and human associated impacts. Associated to this lack of differences in forage offer among natural dynamic phases, the livestock occurrence (guanacos and livestock) do not vary in the landscape. However, harvesting modifies the forest structure and promote changes in the understory biomass and cover that generate similarities with openland vegetation, and contrary to our expectations, light thinning allows to obtain more forage offer, while avoid the loss of naturalness. Our results highlight the correlation between the impact degree of harvesting and the understory development, but also showed a mismatch between forage offer and livestock occurrence. The study of forage quantity and quality, as well as domestic and native stocking rate, generate useful knowledges that could be added to the study of forest structure variables, and should be considered in the design of different management strategies. Much research and monitoring (e.g. forage quality of particular species, causes of under/overgrazing in some areas) are still required to develop and optimize new silvopastoral proposals for a wide variety of management and conservation objectives, and elucidate all the variables that influence over livestock uses.

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Declarations

Conflict of interest The authors have declared no conflict of interest.

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