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Changes in forest structure values along the natural cycle and different management strategies in *Nothofagus antarctica* forests

Guillermo J. Martínez Pastur [a,*], Yamina M. Rosas [a], Jimena Chaves [a], Juan M. Cellini [b], Marcelo D. Barrera [b], Santiago Favoretti [c], María V. Lencinas [a], Pablo L. Peri [d]

[a] *Centro Austral de Investigaciones Científicas (CADIC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Houssay 200, (9410) Ushuaia, Tierra del Fuego, Argentina*

[b] *Universidad Nacional de la Plata (UNLP), Calle 60 y 118, (1900) La Plata, Buenos Aires, Argentina*

[c] *Universidad Nacional de Tierra del Fuego (UNTDF), Fuegia Basket 251, (9410) Ushuaia, Tierra del Fuego, Argentina*

[d] *Instituto Nacional de Tecnología Agropecuaria (INTA), Universidad Nacional de la Patagonia Austral (UNPA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), cc 332, (9400) Río Gallegos, Santa Cruz, Argentina*

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A B S T R A C T

Ecologically sustainable forest management aims to preserve ecosystem integrity by providing wood and non-wood values. For this, it is necessary to determine the losses produced by the different management practices in natural forest resilience. The aim was to determine changes in forest structure values along the natural cycle and human impacts generated by rural timber, pastoral and silvopastoral uses in managed, unmanaged, and transformed *Nothofagus antarctica* forests of Tierra del Fuego (Argentina), as well as in some associated environments (grasslands). We sampled 145 sites to determine landscape characterization, microclimate, soil properties, debris, forest structure and regeneration under different conditions: (i) six phases of natural forest dynamic (even-and uneven-aged), (ii) four types of management and conversion alternatives with and without natural regeneration, and (iii) forest edges and grasslands. Main results showed that stand characteristics (abiotic, soil, forest structure, and regeneration) did not significantly change along the different natural forest phases in even- and uneven-aged structures. However, many studied variables strongly varied depending on harvesting intensities and fire occurrence. The magnitude of these changes was directly related to the impact degree. Multivariate analyses showed a close relationship among the different natural forest phases, and how stands with harvesting or different conversion intensity differ from the control stands, or how much they become similar to openlands. Through different indexes, we related the modifications of the stand characteristics with the magnitude and direction of the changes. Then, these could be used to propose sustainable forest management strategies in the framework of silvopastoral systems.

1. Introduction

Forest structure and overstory composition of native forest stands change across the landscape according to tree species ecology, regional climate, topography, and natural disturbances (e.g. wind, landslides) (Hakkenberg et al., 2016). At high latitudes, temperate natural forests show simple horizontal and vertical structures, usually with few dominant species and with one or two overstory strata, following predictable forest dynamic paths. This occurs in *Nothofagus antarctica* (Forst. f.) Øerst. (commonly named ñire) forests in Tierra del Fuego (Argentina), which grow in pure stands and regenerate by seeds or root sprouts under gap dynamics (Peri et al., 2016a). These native forests can present even- or uneven-aged structures depending on the stand dynamic history, e.g. massive wind-blown leads to even-aged structures, while gap dynamics leads to uneven-aged structures (Ivancich, 2013; Peri et al., 2017).

Forests had been considered in the past as the main obstacle for agriculture and livestock farming, and the first settlers that arrived to Tierra del Fuego removed them through clear-cuts and fires, and sawn adventive grasses with high growth and palatability (Gea et al., 2004; Martínez Pastur et al., 2017). Because natural fires do not occur in the Fuegian archipelago, ñire forests are not naturally adapted to this impact (Veblen et al., 2011; Peri et al., 2017). Nowadays, the preservation of

* Corresponding author.
E-mail addresses: gpastur@conicet.gov.ar (G.J. Martínez Pastur), jmc@agro.unlp.edu.ar (J.M. Cellini), mbarrera@agro.unlp.edu.ar (M.D. Barrera), sfavoretti@untdf.edu.ar (S. Favoretti), mvlencinas@conicet.gov.ar (M.V. Lencinas), peri.pablo@inta.gob.ar (P.L. Peri).

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native forests becomes an important goal in forest management, in order to preserve biodiversity and multiple ecosystem services (ES) provided to society (Perera et al., 2018; Martínez Pastur et al., 2020a). In this context, silvopastoral systems that combine livestock production and timber harvesting are the best strategy to manage the ñire forests (Peri et al., 2016a). Silviculture treatments propose to simplify the natural structures, to open the canopy and maintain homogeneous tree and age distributions, which provide animal shelter and wood production (Martínez Pastur et al., 2018). This management increases the provision of some ES (e.g. animal and timber production) and decreases other services (e.g. supporting or regulating) (Martínez Pastur et al., 2017), and significantly modifies the biodiversity as well as many ecosystem functions, such as nutrient return and mineralization, seed production and predation (Bahamonde et al., 2013, 2015; Peri et al., 2016b; Soler et al., 2017).

Human activities affect ecosystem resilience, which can lead to permanent modifications in the structure and functions (Peri et al., 2017). Stand modifications can lead to positive synergies (e.g. to increase the provisioning ES) but also trade-offs with other ES that generate losses or resilience facing human or natural impacts (e.g. climate change) (Gyenge et al., 2011). Therefore, it is desirable to maintain the natural values of managed stands instead of hybrid or novel ecosystems (Higgs et al., 2017; Evers et al., 2018). Forest management and pastoral uses must be clearly designed to maintain the sustainability in the long term, assuring the persistence capacity of the ecosystems (Schröter et al., 2017; Siry et al., 2018). The persistence capacity is mainly related to the natural regeneration of the native forests, which occurs by seeds or root sprouts in ñire (Peri et al., 2016a, 2017; Bahamonde et al., 2018; Soler et al., 2013, 2018). The addition of adventive grasses to enrich and improve forage quality that modify plant competition/facilitation in the understory, the livestock overgrazing, and the negative synergies between domestic and native herbivore species (e.g. *Lama guanicoe*) (Soler et al., 2013; Martínez Pastur et al., 2016a), may generate strong limitations for the forest persistence in the long-term (Peri et al., 2017). Thus, natural regeneration dynamic was commonly used as proxy to define better management strategies (Strassburg et al., 2016; Siry et al., 2018; Lohbeck et al., 2020).

Ecologically sustainable forest management is proposed as a solution for many ecological and socio-economic problems associated with forest uses (Perera et al., 2018). It aims to preserve ecosystem integrity together with wood and non-wood providing services by maintaining forest structural complexity, species diversity and composition, and ecological processes and functions within the normal disturbance regimes (Lindenmayer et al., 2012). For this, multiple aspects must be considered to achieve the defined forest management objectives, as well as to propose new management alternatives, e.g. sustainable silvopastoral systems must reach a balance between different ES (maximizing provisioning and minimizing the losses in regulating, supporting and cultural) as well as in biodiversity conservation values (Martínez Pastur et al., 2017; Peri et al., 2017). To attain this, we need to determine losses in forest structures values and potential decreases in the resilience of stand recovery through their natural regeneration, and in consequence the maintenance of several ES, biodiversity values and other desirable ecosystem functions. Therefore, the objective of the present work was to determine changes in the forest structure values within the natural cycle and under human impacts generated by rural timber, pastoral and silvopastoral uses in ñire forests of Tierra del Fuego (Argentina). We intent to answer the following questions to develop better management strategies: (i) do the stand characteristics (microclimate, soil, forest structure, and regeneration) change across the different natural forest phases in even- and uneven-aged structures?, (ii) do these stand characteristics change across the different harvesting intensities or fire occurrence?, and (iii) do these stand characteristics differ to those in the associated environments? We propose that knowledge about magnitude and direction of changes due to the modification of the stand characteristics would allow to improve the development of forest management strategies for sustainable silvopastoral use, and to reach a balance between ES (maximizing provisioning and minimizing the losses in regulating, supporting and cultural), as well as to conserve biodiversity.

2. Methods

2.1. Study area

The study area covers most of the natural distribution of ñire forests in the Argentinean sector of Tierra del Fuego (53°38′ to 54°37′S, 66°28′ to 68°36′W), that includes 181.5 thousand ha of pure forests (Collado 2001). This forest type presents different structures (even-aged or uneven-aged) depending on natural (e.g. gap dynamics, windstorms) and human-derived impacts during the last century (e.g. fires, harvesting, conversion to pastures) (Peri et al., 2016a, 2016b). We sampled 145 locations (Fig. 1) including pure ñire forest stands and associated open areas with at least 2 ha with homogeneous characteristics, where also several variables of the landscape were estimated: climate (MT = mean annual temperature, and MR = mean annual rainfall) obtained from WorldClim database (Hijmans et al., 2005), topography (ALT = altitude) using digital elevation models (Farr et al., 2007), and the net primary productivity (NPP) according to the models proposed by Zhao and Running (2010).

2.2. The rationale of the research

The studied forests follow a simple natural dynamic, based on gaps that can generate even- or uneven-aged structures depending on tree recruitment over time in the stands (Ivancich, 2013; Peri et al., 2017; Martínez Pastur et al., 2020b). It was possible to identify four even-aged phases during the natural growth life-cycle (Fig. 2): (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) (Ivancich 2013). While an even-aged stand contains >70% of the basal area (BA) belonging to one growth phase, the uneven-aged stands are mostly bi-modals, where >70% BA is represented with two growth phases. These uneven-aged stands were classified in: (v) young uneven-aged (YUA) when IGP or FGP are the main growth phases in the stand (n = 11 stands), and (vi) mature uneven-aged (MUA) when MAT and DEC growth phases are mixed (n = 9 stands). From these, we selected the MAT forests as a control because this phase best represents the most developed in the natural dynamic, being the most representative at landscape level in Tierra del Fuego (Argentina).

Usually, FGP and MAT stands, and also YUA or MUA, depending on accessibility or closeness to ranch facilities, are harvested for lumber or local timber uses (e.g. rural fencing and small constructions). In this study, we classified the harvested stands according to the harvesting intensity and the response of the natural regeneration (recruitment and survival of the pre-established seedlings/saplings both from root sprouting or seeds) (Fig. 2): (vii) low intensity harvesting (LH) when remnant BA is >30 m^2 ha^{-1} and despite its natural regeneration (n = 27 stands), (viii) high intensity harvesting with regeneration (HHR) with remnant BA < 30 m^2 ha^{-1} and presence of regeneration in the understory despite its density (seedlings defined as <1.3 m height or saplings defined as >1.3 m and less than 5 cm diameter at breast height, DBH) (n = 15 stands), (ix) high intensity harvesting without presence of regeneration in the understory (HHWR) (n = 16 stands), (x) clear-cuts with regeneration (CCR) with remnant BA is <5 m^2 ha^{-1} and with regeneration in the understory (seedlings and/or saplings) (n = 5 stands), and (xi) clear-cuts without regeneration (CCWR) (n = 4 stands).

In Tierra del Fuego, all fires are related to human causes, both accidentally or intentionality. Intentional fires are generated to decrease or eliminate forest cover and promote forage for livestock production. Despite the intensity of the fires, these impacted forests (Fig. 2) were

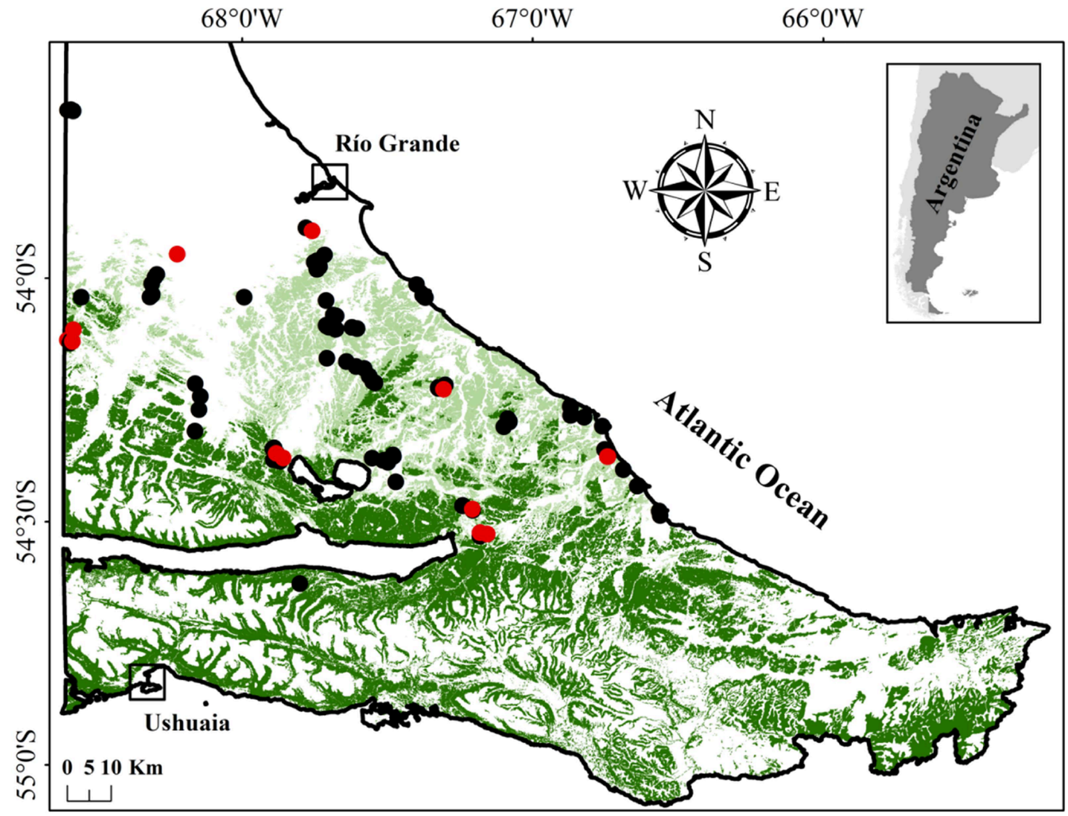

Fig. 1. Location of the study area at the southern portion of Argentina, identifying the distribution of the sampling plots by dots (n = 145), where the control plots are marked with red dots (mature forests, n = 12 stands). *Nothofagus antarctica* forests are represented in light green, while *N. pumilio* and mixed evergreen forests are represented in dark green (extracted from Collado 2001). Main cities are identified with squares. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

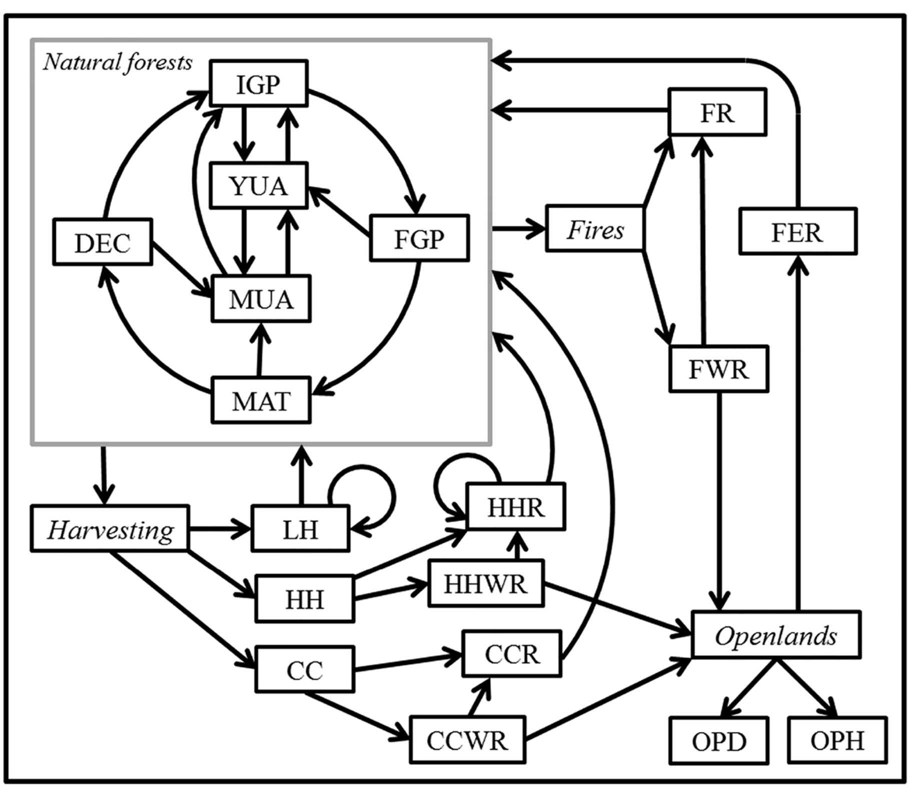

Fig. 2. Rationale of the research study indicating the natural dynamic phases and their relationships in the *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (Argentina). (i) Natural dynamics forests: IGP = initial growth phase, FGP = final growth phase, MAT = mature phase (control treatment), DEC = decay phase, YUA = young uneven-aged, and MUA = mature uneven-aged. (ii) Harvesting and the success of the natural regeneration: LH = low intensity harvesting, HH = high intensity harvesting (HHR = with regeneration, and HHWR = without regeneration), and CC = clear-cuts (CCR = with regeneration, and CCWR = without regeneration). (iii) Forests with fires: FR = with regeneration, and FWR = without regeneration. (iv) Openlands in forested landscapes: OPD = dry grasslands, OPH = humid grasslands, and FER = forest edge regeneration. Arrows indicate the expected evolution between phases.

classified in this study as: (xii) forests affected by fires with regeneration (FR) (n = 4 areas), and (xiii) forests affected by fires without regeneration (FWR) (n = 4 areas). Finally, we included in the comparisons some associated environments that ranchers use in the landscape where ñire forests occurred: (xiv) forest edge regeneration (FER) defined as areas where forests advance over the openlands (n = 13 areas), (xv) openlands dominated by tussock grasslands (OPD) of *Festuca gracillima* and *Empetrum rubrum* surrounding by forest patches (n = 6 areas), and (xvi) openlands dominated by wetlands (OPH) of *Juncus scheuzeroides*, *Carex curta*, *C. macloviana* and *Caltha sagittata* close to streams and surrounding by forest patches (n = 4 areas).

2.3. Sampling of the stands

In each forest stand or openland area, we placed at random a 50 m transect to characterize each site in the middle summer (January to February). Canopy structure and solar radiation transmission were measured using hemispherical photographs taken in the center of each transect at ground level with an 8-mm fish eye lens (Sigma, Japan) mounted on a 35 mm digital camera (Nikon, Japan) with a tripod leveling head to ensure horizontal lens position. Each photograph was orientated with the upper edge towards the magnetic north, avoiding direct sunshine under evenly overcast skies or cloudless days. Gap Light Analyzer software v.2.0 (Frazer et al., 2001) was used to define overstory crown cover (CC) as a percentage of open sky relative to the cover, relative leaf area index (LAI), and total radiation at understory level (TR) as the amount of direct and diffuse radiation transmitted through canopy. The user-supplied input variables and radiation details are presented in Martínez Pastur et al. (2011).

Four soil samples (0–10 cm depth) were randomly collected along each transect using a field borer with known volume (230.9 cm^3) after previously remove the litter layer. Samples were weighted before and after air-drying in laboratory conditions (24 °C) until constant weight. Soil bulk density (SBD) and soil water content (SWC) were obtained from the average of the four samples. After that, coarse root debris >2 mm and soil aggregations (e.g. small stones and large sand-sized) had been removed by sieving. 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 we determined: (i) soil acidity (pH) by using a pH-meter in soil water suspension (air-dried samples and deionized water) with a soil:water ratio of 1:2.5 (Bao, 2000); (ii) total organic carbon (C) from soil samples washed with HCl (50%) by an automatic analyzer (LECO CR12, USA); (iii) total nitrogen (N) by a semi-micro Kjeldahl method; and (iv) extractable phosphorous (P) according to the method of Bray and Kurtz (1945). Data for nutrient contents were presented as kg m^{-2} in the first 30 cm depth, using the SBD data of each stand.

Forest structure was characterized by two plots located at the beginning and the end of each transect, using the point sampling method (BAF = 1–5) (Bitterlich, 1984) with a Criterion RD-1000 (Laser Technology, USA). In each sampling-point we measured to each tree: (i) diameter at breast height (DBH) with a forest caliper; (ii) development phase (IGP, FGP, MAT, DEC) (based on Ivancich 2013); and (iii) vigor (VIG) (1–3, where higher values indicated more crown vitality). Also, we estimated (iv) dominant height (DH) of the stand, using a TruPulse 200 laser clinometer and distance rangefinder (Laser Technology, USA) by averaging height of the two taller trees per transect. These data allowed us to determine the site quality (SQ), tree density (TD), basal area (BA), total over bark volume (TOBV), and mean total volume annual growth (GRO) of each stand, following Peri et al. (2010) and Ivancich et al. (2011, 2014). For further analyses, the stands were classified according to the different age structures (proxy: development phase of the trees). For this, we consider the basal area of the trees for the different development phases, and classified them as was described before in Fig. 2.

To evaluate the understory structure, we used the point-intercept method (Levy and Madden, 1933) with 50 intercept points (every 1 m) along each transect. In each point, we recorded intercepted vascular plant species (data not shown), bare soil or litter without vegetation (BS), and woody debris cover (DC) (>2.5 cm diameter) to calculate ground cover. Then, debris volume (DV) was estimated by multiplying the diameter of the intercepted debris and its cover (relative area) that debris occupied in the stand floor. Moreover, we measured tree regeneration density and height (from the base to the top of the longest extended shoot), sorted by (i) initial regeneration (IR) including recruitment (REC) of 1-year-old and seedlings, and (ii) advanced regeneration (AR) including saplings with more than 1.3 m height and <5.0 cm DBH. IR was measured in two 1 m^2 plots, while AR was measured in two 5 m^2 at the beginning and the end of each transect. With these data, total density (TDIR, TDAR) and the mean height (HIR, HAR) for the regeneration were calculated. In each regeneration plant, we also determined browsing damages (BRO) due to native populations of *Lama guanicoe* (guanaco) or domestic livestock, and abiotic damages (AD) due to spring frost or summer dryness. Finally, the quality of the AR (QAR) was characterized though the vigor, stem shape, defects, and health of each plant.

Finally, three indexes were constructed to compare the different stand conditions. For this, the variable values were standardized between 0 and 1 (the minimum and the maximum observed values considering all the plots), and each index was defined as the average value of each set of variables: (i) the forest structure index (FI) which include CC, LAI, DH, SQ, VIG, TD, DBH, BA, TOBV, and GRO; (ii) the microclimate, soil properties and debris index (EI) which include TR, SWC, SBD, C, N, P, pH, BS, DC, and DV; and (iii) the forest regeneration index (RI) which include TDIR, HIR, REC, BRO, AD, TDAR, HAR, and QAR. The absence of a particular variable value (e.g. seedling height, where no seedlings exists) was represented by zero in the index construction to balance the outputs in the different comparisons. Standard error of indexes for each different stand condition was also calculated for further comparisons.

2.4. Statistical analyses

We defined four treatments, each one with several levels: (i) the natural dynamic cycle (IGP, FGP, YUA, MUA, MAT, DEC), (ii) the intensity of the interventions and the response of the natural regeneration (MAT, LH, HHR, HHWR, CCR, CCWR), (iii) fires and the response of the natural regeneration (MAT, FR, FWR), and (iv) associated environments (MAT, FER, OPD, OPH). We used one-way ANOVAs to test the differences, which were conducted using Fisher test and Tukey test at $p < 0.05$ to separate means. Using these treatments and levels we analyzed the following variables: (i) landscape (MT, MR, PPN, ALT), (ii) microclimate, soil properties and debris (TR, SWC, SBD, C, N, P, pH, BS, DC, DV), (iii) forest structure (CC, LAI, DH, SQ, VIG, TD, DBH, BA, TOBV, GRO), and (iv) forest regeneration (TDIR, HIR, REC, BRO, AD, TDAR, HAR, QAR).

Principal Component Analysis (PCA) was performed to analyze multivariate relations among treatments considering: (i) the natural dynamic cycle, (ii) the intensity of the interventions and the response of the natural regeneration compared to the control (MAT), and (iii) fires, associated environments and the response of the natural regeneration compared to the control (MAT). In each PCA, we analyzed the whole group of variables (10 of microclimate, soil properties and debris, 11 of forest structure, and 8 of forest regeneration), but only those with low redundancy and higher correlation (eigenvalues up to 0.300 in the first axis in one of the three conducted analyses) were used. 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. These analyses were conducted in PCORD 5.0 (McCune and Mefford, 1999).

3. Results

Climate and landscape characterization of the sampled stands (Table 1) did not present significant differences among the natural cycle treatment, meaning the studied levels are equally distributed across the territory, and also did not present significant differences with the control (MAT). Contrary to this, the levels defined in the harvesting treatment presented significant differences among them. Harvesting was conducted in drier areas at lower altitudes than MAT (e.g. clear-cuts were conducted in areas with 365–391 mm yr^{-1} rainfall at <85 m a.s.l. compared to 419 mm yr^{-1} rainfall at 135 m a.s.l. in the control). Also, the net primary productivity of the stands significantly changed among the levels due to harvesting intensity, from 310 to 489 gr C m^{-2} yr^{-1}. Fire treatment did not present significant differences across the landscape either, but in the openlands, air temperature was higher, and rainfall and altitude lower than in the control plots. However, net primary productivity (NPP) did not show differences compared with the control.

Microclimate of the sample sites was characterized with the total radiation at understory level and the soil water content at 10 cm depth (Table 2). Total radiation showed significant differences in all the studied treatments. In the natural cycle treatment, stands with young trees (IGP, FGP, YUA) presented lower radiation levels than stands with older trees. Also, total radiation was directly related to the harvesting or fire intensity, increasing by more than 2 times in clear-cuts or intensive fires. However, soil moisture did not change in landscape, evidencing a great local variability in the studied levels and treatments (e.g. YUA vs. MAT, or OPD vs. OPH). There were not significant differences in soil properties among the natural cycle treatment and fire occurrences, evidencing that the different development phases (IGP, FGP, MAT, DEC) or even- or uneven-aged forest types maintain common soil characteristics. However, soil bulk density significantly increased with harvesting, but was not clearly related with the intensity (0.54 g cm^{-3} in control compared to 0.68–0.80 g cm^{-3} in harvested areas). Soil nitrogen and phosphorous content also changed due to harvesting, decreasing in light and heavy harvesting compared to the control treatment. However, the nitrogen content increased in clear-cuts compared to the control, and phosphorous presented the lowest values among all the levels. Finally, while bare soil cover did not vary among treatments and levels, debris cover and volume were higher in the fire treatment compared with openlands. Fire intensity influenced on debris cover, and control treatment presented more debris than the openlands.

Forest structure showed significant differences in most variables across the different studied treatments (Table 3). Natural cycle significantly changed the variables according to the ratio of younger and older trees in their stand composition. Crown cover and LAI are inversely related to total radiation, being the canopy more closed where young trees are more abundant. Mean tree vigor was also higher in young stand growth phases. There were no significant differences in dominant height and site quality with the control (MAT), evidencing that the sampled stands were equally distributed across the territory, and not presented significant differences with the control (MAT). As it was expected, the development phases had influenced tree size and biomass accumulation, where younger stands presented higher tree density, lower basal area, total over bark volume, and higher growth volume than mature stands. These values determined for the different phases allowed us to define the thresholds for the natural cycle treatments, which can be possible to find in natural landscapes without impacts in the forest structure.

Harvesting significantly modified the forest structure (Table 3), depending on cut intensity. Low intensity cut (LH) was not significantly different from the control, indicating that the harvesting impact was similar to those produced by the natural dynamics (e.g. gaps) or showing a quick forest structure recovery. The high harvesting intensity (HHR and HHWR) greatly diminished forest structure values (CC, LAI, TD, BA, TOBV), generating a loss of 40% in stand growth volume. Clear-cuts presented similar trend by reducing forest structure values (e.g. basal area <2 m^2 ha^{-1}, crown cover <20%, and growth volume <0.1 m^3 ha^{-1}). It is interesting to note that clear-cuts were conducted in low site qualities (4.6–4.8), where forests usually do not include timber values. As was expected fires influenced forest structure values of the impacted stands (Table 3). Fire decreased tree cover (CC and LAI), basal area, stand volume, and in consequence, affected volume growth of the stand. Finally, as it was expected openlands presented the lowest forest structure values (Table 3). However, it is interesting to highlight the recovery of the variables where forest regeneration advance in the forest edges (FER).

Recruitment and initial regeneration did not significantly change among different natural cycle levels, evidencing that seedling bank occurred homogeneously across the landscape (Table 4). The damage in the regeneration, including browsing (guanaco and livestock), frosting and dryness, did not varied among the natural cycle levels either. However, total density of advanced regeneration increased in young phase (IGP > other levels), but did not the other characteristics (HAR and QAR). As was expected, the levels without regeneration in the harvesting treatment (HHWR and CCWR) significantly differed from control and other cutting forests (LH, HHR and CCR). Clear-cuts showed significantly higher plants of initial regeneration, evidencing some positive response to the canopy opening, but with higher browsing damage. Advanced regeneration density only showed significant differences between control and high intensity harvesting treatment. When regeneration occurred in the stands affected by fires (FR), the values were not different from those found in the control. Finally, in the comparisons with the associated environments, openlands differed from the studied forest levels, and the regeneration of the forest edges was not significantly different (in quantity and quality) to those found in the control.

The described differences in the studied variables (Tables 2–4) were combined and summarized in the following analyses (Figs. 3 and 4).

Table 1
ANOVAs for the different treatments and levels (see acronyms in Fig. 2) characterizing climate, productivity and topography of the landscape where plots were measured in *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (Argentina). MT = mean annual temperature, MR = mean annual rainfall, NPP = net primary productivity, and ALT = altitude.

Treatment	Levels	MT (°C)	MR (mm yr^{-1})	NPP (gr C m^{-2} yr^{-1})	ALT (m a.s.l.)
Natural cycle	IGP	5.1	429.0	410.6	103.0
	FGP	5.0	406.8	393.4	125.5
	YUA	5.1	387.8	317.6	100.6
	MUA	5.1	399.0	401.4	96.3
	MAT	5.0	418.8	310.3	134.6
	DEC	4.8	404.4	303.4	134.2
	F(p)	*1.20 (0.325)*	*1.32 (0.275)*	*1.93(0.109)*	*0.95(0.462)*
Harvesting	MAT	5.0	418.8b	310.3a	134.6b
	LH	5.1	390.6a	315.0a	116.2ab
	HHR	5.1	402.3ab	335.7ab	130.7b
	HHWR	5.1	380.5a	332.6ab	88.5a
	CCR	5.1	364.6a	397.9ab	80.2a
	CCWR	5.2	391.2ab	489.1b	84.5a
	F(p)	*0.85 (0.518)*	*4.23 (0.002)*	*2.78(0.024)*	*3.59(0.006)*
Fire	MAT	5.0	418.8	310.3	134.6
	FR	5.1	382.7	351.0	85.0
	FWR	5.1	414.7	285.8	113.0
	F(p)	*0.73 (0.496)*	*1.53 (0.244)*	*0.69(0.513)*	*2.42(0.119)*
Openlands	MAT	5.0a	418.8b	310.3	134.6b
	FER	5.1a	423.2b	371.6	111.8b
	OPD	5.1a	374.0a	333.9	61.5a
	OPH	5.4b	369.0a	224.1	44.8a
	F(p)	*10.39 (0.001)*	*6.32 (0.003)*	*1.59(0.218)*	*22.99 (<0.001)*

F = Fisher test, p = probability at p < 0.05.

Table 2
ANOVAs for the different treatments and levels (see acronyms in Fig. 2) characterizing microclimate, soil properties and debris of the plots measured in *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (Argentina). TR = total radiation at understory level, SWC = soil water content, SBD = soil bulk density, C = soil carbon content, N = soil nitrogen content, P = soil phosphorous content, pH = soil acidity, BS = bare soil, DC = debris cover, DV = debris volume in the forest floor.

Treatment	Levels	TR ($W\ m^{-2}$)	SWC (%)	SBD ($g\ cm^{-3}$)	C ($kg\ m^{-2}$)	N ($kg\ m^{-2}$)	P ($kg\ m^{-2}$)	pH	BS (%)	DC (%)	DV ($m^3\ ha^{-1}$)
Natural cycle	IGP	11.9ab	35.5	0.68	18.0	1.23	0.54	4.23	9.5	17.0	69.7
	FGP	6.75a	50.5	0.56	17.6	1.06	0.38	4.59	14.0	17.0	70.0
	YUA	11.7ab	30.3	0.66	14.9	0.88	0.50	4.92	7.5	11.8	69.9
	MUA	15.6b	47.4	0.63	17.9	0.95	0.34	5.05	4.4	12.2	84.7
	MAT	16.6b	76.4	0.54	16.5	1.04	0.48	5.02	4.2	14.2	88.4
	DEC	13.4ab	36.2	0.72	17.1	1.02	0.53	4.86	3.2	13.6	106.0
	F(p)	*3.01(0.021)*	*0.63 (0.678)*	*1.44 (0.232)*	*0.99 (0.436)*	*1.23 (0.311)*	*0.77 (0.576)*	*1.78 (0.139)*	*1.61 (0.180)*	*0.53(0.753)*	*0.41 (0.837)*
Harvesting	MAT	16.6a	76.4	0.54a	16.5	1.04ab	0.48b	5.02	4.2	14.2	88.4
	LH	11.7a	32.9	0.69ab	16.0	0.92a	0.46b	4.97	5.4	13.9	81.5
	HHR	26.4ab	34.4	0.70ab	16.8	0.98ab	0.36ab	4.74	4.1	12.0	73.0
	HHWR	24.4ab	29.6	0.80b	17.5	0.95ab	0.49b	4.84	7.8	11.4	64.7
	CCR	33.9b	35.9	0.68ab	16.1	1.17ab	0.23a	5.13	2.0	10.4	92.7
	CCWR	34.4b	42.2	0.69ab	18.5	1.31b	0.22a	4.93	1.5	11.5	77.6
	F(p)	*27.06 (<0.001)*	*1.55 (0.184)*	*4.10 (0.003)*	*0.63 (0.674)*	*2.92 (0.018)*	*2.51 (0.037)*	*0.85 (0.516)*	*0.91 (0.479)*	*0.55(0.735)*	*0.37 (0.867)*
Fire	MAT	16.6a	76.4	0.54	16.5	1.04	0.48	5.02	4.2	14.2b	88.4
	FR	29.1b	59.9	0.53	12.6	0.94	0.25	5.04	2.0	3.0a	14.7
	FWR	35.7b	26.1	0.67	14.8	1.06	0.77	5.87	8.5	14.0ab	104.1
	F(p)	*20.70 (<0.001)*	*1.22 (0.321)*	*0.59 (0.566)*	*1.22 (0.320)*	*0.24 (0.791)*	*2.11 (0.151)*	*3.44 (0.058)*	*1.41 (0.271)*	*3.90(0.040)*	*2.51 (0.111)*
Openlands	MAT	16.6a	76.4	0.54ab	16.5	1.04a	0.48b	5.02	4.2	14.2b	88.4b
	FER	33.9b	78.6	0.59ab	18.7	1.42b	0.27ab	4.41	5.6	0.4a	0.8a
	OPD	37.9b	26.1	0.73b	15.0	0.76a	0.36ab	4.66	9.7	0.0a	0.0a
	OPH	36.1b	133.8	0.30a	18.7	1.11ab	0.15a	5.04	0.0	0.0a	0.0a
	F(p)	*39.30 (<0.001)*	*1.07 (0.382)*	*5.23 (0.007)*	*1.29 (0.303)*	*6.18 (0.003)*	*4.99 (0.008)*	*2.85 (0.059)*	*2.02 (0.139)*	*20.02 (<0.001)*	*10.43 (0.001)*

F = Fisher test, p = probability at $p < 0.05$.

Table 3
ANOVAs for the different treatments and levels (see acronyms in Fig. 2) characterizing the forest structure of the plots measured in *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (Argentina). CC = crown cover, LAI = leaf area index, DH = dominant tree height, SQ = site quality of the stand, VIG = mean tree vigor, TD = tree density, DBH = diameter at breast height, BA = basal area, TOBV = total over bark volume, GRO = mean total volume annual growth of the stand.

Treatment	Levels	CC (%)	LAI	DH (m)	SQ (1–5)	VIG (1–3)	TD ($n\ ha^{-1}$)	DBH (cm)	BA ($m^2\ ha^{-1}$)	TOBV ($m^3\ ha^{-1}$)	GRO ($m^3\ ha^{-1}\ yr^{-1}$)
Natural cycle	IGP	78.0ab	1.82ab	9.1	3.9	2.3ab	3384ab	11.2a	23.7a	100.2	2.90ab
	FGP	87.3b	2.23b	10.6	3.0	2.5b	3734b	19.2ab	43.0b	212.7	4.64b
	YUA	77.6ab	1.65ab	8.6	4.1	2.1ab	2809ab	24.3ab	34.6ab	153.4	2.46a
	MUA	69.5ab	1.18a	8.9	3.9	1.9a	851a	34.1b	33.3ab	182.5	2.11a
	MAT	67.3a	1.13a	9.2	3.7	1.9a	1099ab	30.5b	31.9ab	165.8	2.19a
	DEC	75.7ab	1.51ab	10.1	3.5	1.9a	981ab	36.2b	42.2ab	229.7	2.64ab
	F(p)	*3.09(0.018)*	*4.46(0.003)*	*0.63 (0.678)*	*0.83 (0.538)*	*4.49 (0.002)*	*8.22 (<0.001)*	*5.47 (0.001)*	*2.93(0.024)*	*2.42(0.052)*	*3.43(0.011)*
Harvesting	MAT	67.3c	1.13b	9.2ab	3.7a	1.9	1099b	30.5	31.9c	165.8c	2.19bc
	LH	76.6c	1.51b	9.8ab	3.5a	2.1	2049b	31.8	38.8c	201.2c	2.98c
	HHR	45.1b	0.51a	10.5b	3.3a	2.0	441ab	37.4	17.6b	105.6b	1.46ab
	HHWR	48.1b	0.61a	9.2ab	3.9a	2.0	531ab	33.3	16.9b	89.6b	1.14ab
	CCR	19.6a	0.09a	7.2ab	4.6b	2.3	26a	30.9	1.9a	9.9a	0.08a
	CCWR	15.2a	0.02a	6.7a	4.8b	2.8	14a	32.2	1.0a	4.5a	0.04a
	F(p)	*31.01 (<0.001)*	*21.02 (<0.001)*	*3.23 (0.011)*	*2.61 (0.032)*	*1.32 (0.267)*	*3.21(0.011)*	*0.69 (0.635)*	*41.06 (<0.001)*	*23.08 (<0.001)*	*11.74 (<0.001)*
Fire	MAT	67.3b	1.13b	9.2	3.7	1.9	1099	30.5	31.9c	165.8b	2.19b
	FR	38.7a	0.31a	8.7	4.2	2.1	739	29.1	17.5b	77.9a	0.98ab
	FWR	16.9a	0.07a	11.8	3.0	2.8	15	53.1	1.5a	8.6a	0.08a
	F(p)	*28.5 (<0.001)*	*14.61 (0.001)*	*1.41 (0.270)*	*1.05 (0.370)*	*3.53 (0.055)*	*3.16(0.067)*	*3.09 (0.075)*	*30.25 (<0.001)*	*14.00 (0.001)*	*10.06 (0.001)*
Openlands	MAT	67.3c	1.13b	9.2	3.7	1.9a	1099b	30.5	31.9b	165.8b	2.19b
	FER	25.8b	0.14a	7.9	4.4	2.7b	21a	11.9	0.4a	1.3a	0.02a
	OPD	11.9ab	0.01a	–	–	–	0a	–	0.0a	0.0a	0.00a
	OPH	0.0a	0.00a	–	–	–	0a	–	0.0a	0.0a	0.00a
	F(p)	*63.06 (<0.001)*	*23.8 (<0.001)*	*0.58 (0.459)*	*1.27 (0.277)*	*9.76 (0.009)*	*8.39(0.001)*	*3.84 (0.073)*	*73.81 (<0.001)*	*28.87 (<0.001)*	*19.74 (<0.001)*

F = Fisher test, p = probability at $p < 0.05$.

Table 4
ANOVAs for the different treatments and levels (see acronyms in Fig. 2) characterizing the forest regeneration in *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (Argentina). TDIR = total density of initial regeneration, HIR = mean height of initial regeneration, REC = recruitment, BRO = browsing of the initial regeneration, AD = abiotic damage of the initial regeneration, TDAR = total density of advanced regeneration, HAR = mean height of advanced regeneration, QAR = forest quality of the advanced regeneration.

Treatment	Levels	TDIR (thousand ha^{-1})	HIR (cm)	REC (thousand ha^{-1})	BRO (%)	AD (%)	TDAR (thousand ha^{-1})	HAR (m)	QAR (%)
Natural cycle	IGP	18.8	50.3	10.0	0.0	0.0	95.0b	4.71	73.8
	FGP	15.0	27.3	7.5	50.0	0.0	0.8a	6.50	99.0
	YUA	57.3	18.0	5.0	0.0	4.2	18.2a	4.13	54.2
	MUA	66.1	28.7	0.0	18.0	2.0	11.7a	2.08	44.6
	MAT	25.8	18.1	0.8	0.0	2.9	12.5a	2.71	41.6
	DEC	74.0	8.1	0.0	14.2	0.0	30.0a	2.83	43.0
	F(p)	*0.61(0.695)*	*0.59(0.709)*	*0.85(0.522)*	*1.65(0.216)*	*0.36(0.866)*	*5.18(0.001)*	*1.75(0.169)*	*0.86(0.526)*
Harvesting	MAT	25.8	18.1a	0.8	0.0a	2.9	12.5b	2.71	41.6
	LH	33.9	16.9a	27.2	12.5ab	0.0	7.6b	3.51	47.1
	HHR	50.0	20.1a	0.0	2.6a	3.4	0.7a	1.36	0.0
	HHWR	0.0	–	0.0	–	–	0.0a	–	–
	CCR	12.0	50.8b	0.0	50.0b	0.0	7.0b	2.62	71.4
	CCWR	0.0	–	0.0	–	–	0.0a	–	–
	F(p)	*0.67(0.647)*	*3.85(0.019)*	*0.39(0.857)*	*3.57(0.027)*	*0.99(0.413)*	*2.52(0.037)*	*1.36(0.286)*	*0.81(0.506)*
Fire	MAT	25.8	18.1	0.8	0.0	2.9	12.5	2.71	41.6
	FR	57.5	30.4	0.0	44.4	4.4	11.2	2.30	56.2
	FWR	0.0	–	0.0	–	–	0.0	–	–
	F(p)	*1.74(0.205)*	*0.85(0.387)*	*0.31(0.738)*	*4.29(0.084)*	*0.13(0.734)*	*1.05(0.372)*	*0.08(0.782)*	*0.17(0.691)*
Openlands	MAT	25.8	18.1	0.8	0.0	2.9	12.5	2.71	41.6
	FER	24.0	3.9	0.0	43.6	0.0	14.0	1.84	48.3
	OPD	0.0	–	0.0	–	–	0.0	–	–
	OPH	0.0	–	0.0	–	–	0.0	–	–
	F(p)	*1.47(0.247)*	*3.50(0.098)*	*0.39(0.763)*	*5.14(0.057)*	*1.71(0.231)*	*2.59(0.077)*	*0.78(0.397)*	*0.07(0.799)*

F = Fisher test, p = probability at $p < 0.05$.

Forest structure index showed a close grouping among the different levels of the natural cycle including the light harvesting (FI × EI and FI × RI in Fig. 3). However, in the FI × RI comparison, IGP evidenced greater differences than the other levels. The natural associated non-forested environments exhibited a contrasting pattern. The studied impacts (harvesting and fires) generated a decrease in the values of FI and a dispersion in the values of EI, increasing the standard error of each level. The distribution of the different treatments and levels are closely related to the impact level (e.g., high impact levels were similar to the openlands). Finally, in the EI × RI comparison, there was not a clear separation among treatments, e.g. stands without natural regeneration or non-forested environments. These results clearly highlighted relationships between regeneration and environmental variables at landscape level.

The different levels of the natural dynamic treatment were mixed in the graphical representation of the PCA (Fig. 4A), although young stands (IGP and FGP) presented a more conspicuous grouping with less dispersion than mature or uneven-aged stands. Eigenvalues for the first two components (Fig. 4A) were 2.590 ($p < 0.001$) and 2.286 ($p < 0.001$) respectively, explaining 43.2% and 81.3% of the cumulative variance of the total dataset. The factors with highest absolute value coefficients for Axis 1 were CC > TR > SQ > TOBV, while those for Axis 2 were DBH > DEN > TOBV > SQ. As was detected in the univariate analyses, CC and DEN were the most related variables with young stands (IGP and FGP), while TR was related to older stands. PCA for forests with harvesting and considering the regeneration success (Fig. 4B) were split in groups, where LH was intermingled with control (CC and TOBV were the variables that better explained their distribution), while in the opposite ordination appeared high intensity harvesting treatments, where TR was the most important associated variable. The stands without regeneration were mixed with those levels with regeneration, but with less dispersion. Eigenvalues for the first two components (Fig. 4B) were 3.220 ($p < 0.001$) and 1.528 ($p < 0.001$), explaining 64.4% and 95.0% of the cumulative variance of the total dataset. The factors with highest absolute value coefficients for Axis 1 were TOBV > CC > TR > DH > SQ, while those for Axis 2 were SQ > DH > TR > CC. Finally, the PCA for forests with fires and openlands (Fig. 4C), showed a very clear separation between mature forest plots, fires with regeneration, and the other treatments. Dry tussock grasslands were a conspicuous group with the lowest dispersion, while fires without regeneration were intermingled with the other openland plots. Eigenvalues for the first two components (Fig. 4C) were 1.872 ($p = 0.002$) and 1.496 ($p < 0.001$), explaining 46.8% and 84.2% of the cumulative variance of the total dataset. The factors with highest absolute value coefficients for Axis 1 were TR > BA, while those for Axis 2 were SM > SBD.

4. Discussion

4.1. Changes in the even- and uneven-aged stands across the natural dynamic phases

The different age-phases of the natural forests occurred across the territory, e.g. even- or uneven-aged stands are intermixed across Argentinean side of Tierra del Fuego, including the full range of stand site qualities. The natural dynamics of these forests follow simple and predictable patterns (e.g. gap dynamics or mass wind-thrown) (Armesto et al., 1992; Rebertus et al., 1997; Veblen et al., 1992, 2011), mainly in patches along the landscape that generate a desirable heterogeneity to improve forest resilience (Levine et al., 2016; Koontz et al., 2020).

Forest structure (e.g. tree diameter, density, stand volume) changed across the natural dynamic cycle (proxy: stand age), consequently influencing microclimate inside the stands. The magnitude and direction of these structural changes were coincident with other well-documented studies (Peri et al., 2010; Ivancich, 2013; Bahamonde et al., 2015, 2018). However, it was very interesting that no clear patterns were found for soil moisture at the landscape level, evidencing the significant role that natural forest cover (despite the stand age) plays over the soil water cycle (del Campo et al., 2017; Sheil, 2018). Also, physic-chemical soil characteristics did not change across the natural dynamic cycle (e.g. comparing young vs. mature stands, or even- vs. uneven-aged stands), evidencing the resilience of ñire forests to the natural disturbances. In fact, the natural seedling bank did not present significant differences along the natural forests without human-derived impacts, neither for browsing levels or abiotic damages (e.g. frosting and dryness) that were

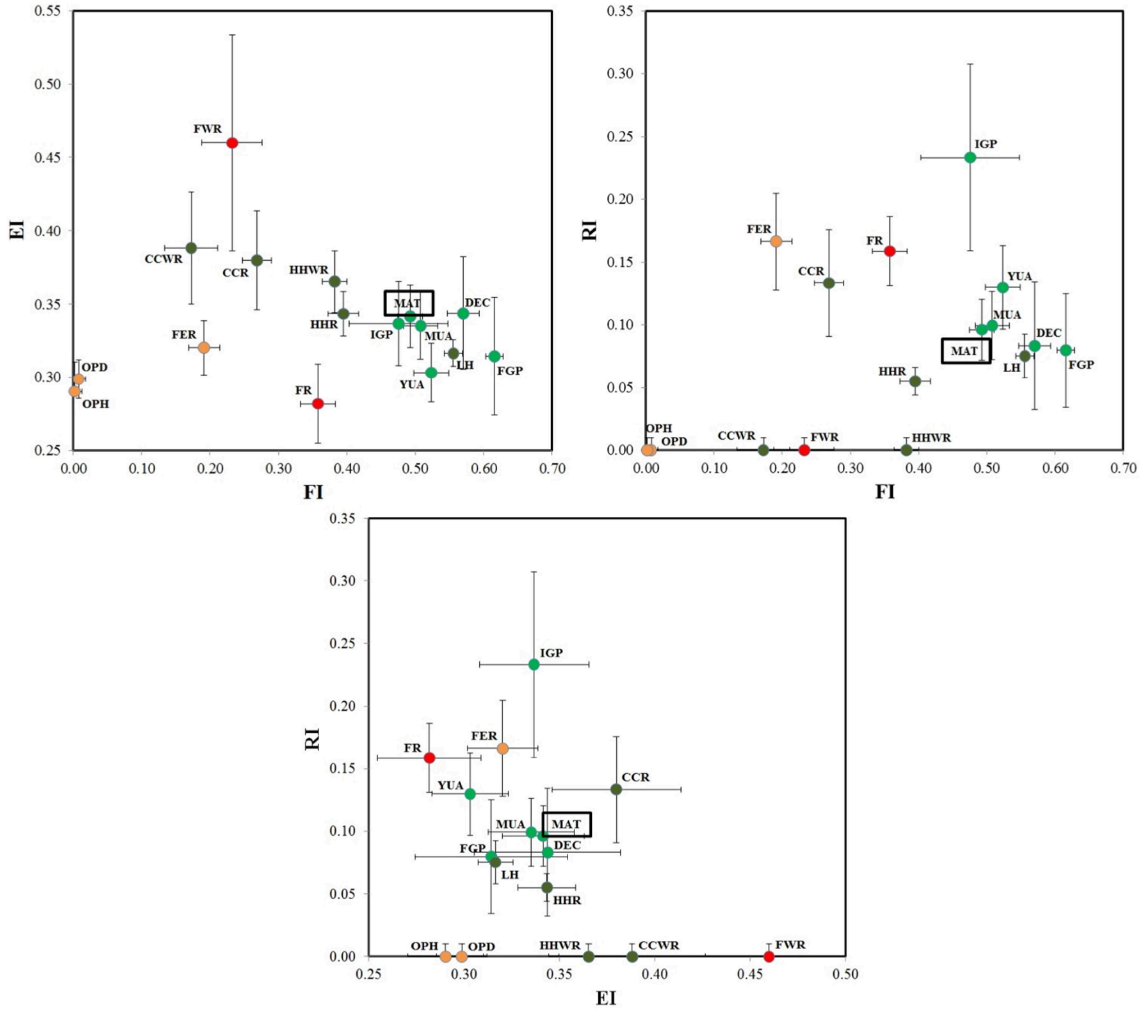

Fig. 3. Relationships among group of variables for the different natural dynamic phases (see acronyms in Fig. 2) of *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (Argentina). FI = forest structure index, EI = microclimate, soil properties and debris index, RI = forest regeneration index. Bars indicate standard error for each axis.

equally distributed across the landscape. In summary, natural forests were close related into a homogeneous group (Figs. 3 and 4).

One of the main challenges for biodiversity conservation and provision of ecosystem services is to define the natural forest structure that best suits these objectives across the landscape. In this sense, the definition of old-growth forest is proposed to highlight the main desirable characteristics of stands for this purpose (Lindenmayer et al., 2006; Wirth et al., 2009). In ñire forests, it was found that uneven-aged structures with prevalence of mature and decay trees sustained more potential biodiversity (Martínez Pastur et al., 2020b). However, in this study we found that other ecosystem services did not greatly change across the different natural forest structures at landscape level (e.g. net primary productivity). Several studies have identified variations in the biodiversity and provision of ecosystem services around the world, when different natural dynamic structures are compared in the same forest type (Hakkenberg et al., 2016; Strassburg et al., 2016; Lellia et al., 2019), highlighting the importance for multi-criteria decision-making (e.g. Martínez Pastur et al., 2017). In summary, the variation of stands under natural dynamic (e.g. in age structures) associated to natural disturbances provides information about the magnitude of impacts that forests can support maintaining their resilience. The assessing of this variations should be considered in base-line studies, to generate enough information about impacts that forests can deal without losing its resilience, which should be a guide for the development of management and conservation strategies (Schnitzler and Borlea, 1998; Siry et al., 2018). However, the range of natural variations is rarely considered in proposals of sustainable management, which could be also enriched including long-term perspective studies. This approach could have important management implications, since can allow to improve and deepen specific recommendations to achieve sustainability (e.g. Noss, 1999; Tierney et al., 2009; Peri et al., 2016b).

4.2. *Forest harvesting and human induced fires: how much we can pressure over the natural forests?*

The rationale of our research study (Fig. 2) showed a close relationship of the natural forests, as was described in our results, where regeneration was enough to recover the impacts of the natural losses across the life cycle (Soler et al., 2013, 2018; Peri et al., 2017; Bahamonde et al., 2018). Harvesting generated different pathways depending on cut intensity and frequency and the success of natural regeneration. In Tierra del Fuego, management proposals induce a wide range of modifications in the natural forests, from small impacts (e.g. canopy opening by cutting single trees through selective cuttings) to the conversion of the forests into grasslands for livestock (e.g. clear-cuts or fires to remove all the trees) (Gea et al., 2004). As was stated by Rosas et al. (2021), harvesting is spatially heterogeneous, being higher near cities, ranches and routes. Correlated with that, we found differences

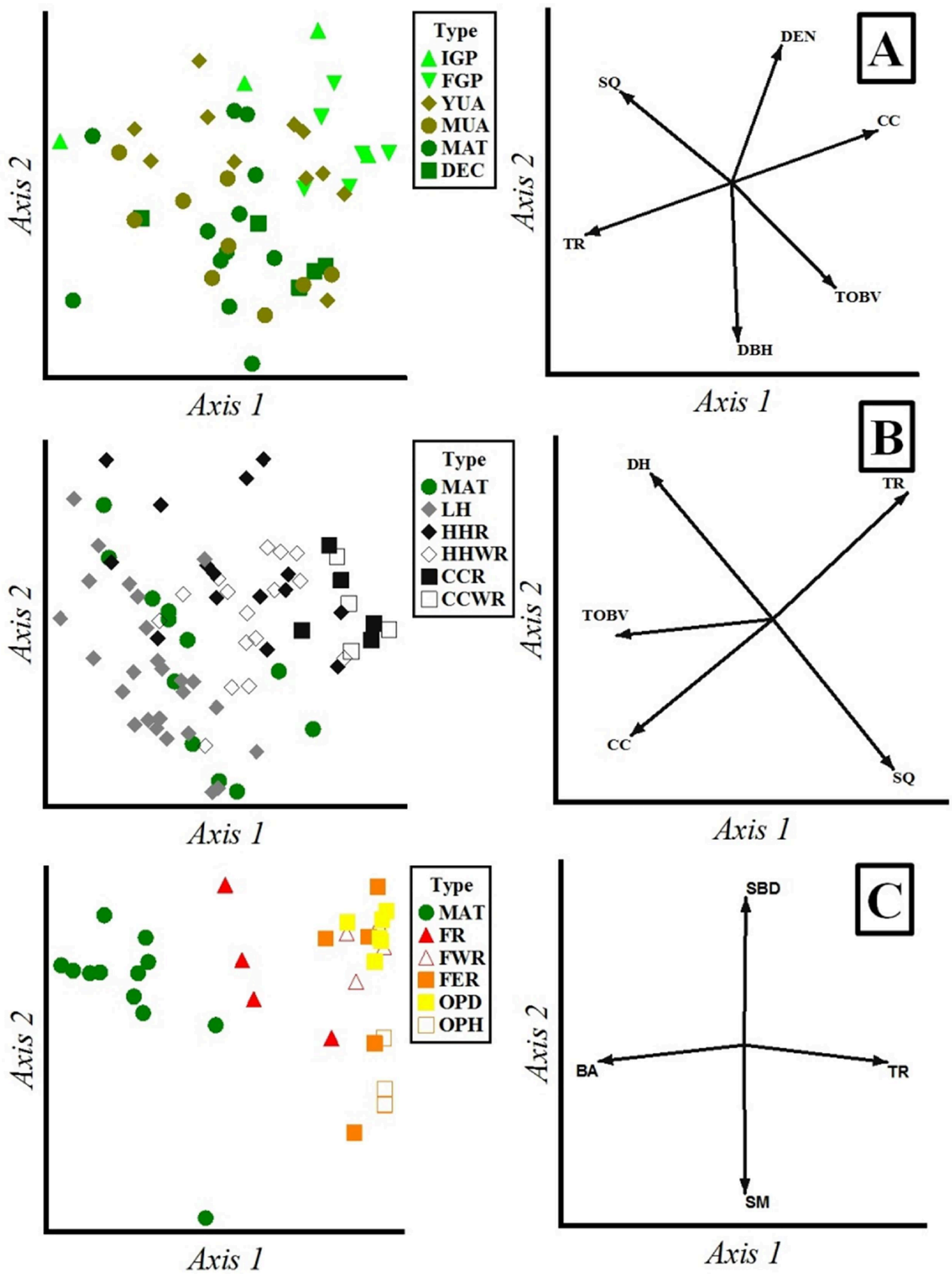

Fig. 4. PCA considering the natural dynamics phases (A), the harvesting and the success of the natural regeneration (B), and forests with fire (regeneration success are not discriminated in the analysis) and openlands in forested landscapes (C) of *Nothofagus antarctica* forests and associated environments of Tierra del Fuego (Argentina) (see acronyms in Fig. 2 and Tables 2–4).

along the landscape in variables related to harvesting intensity (Table 1), mainly in northern forests close to ecotone grasslands where ranching is more intense (less rain at low altitude but with more net primary productivity) (Martínez Pastur et al., 2017). On the other hand, low intensity harvesting (LH) emulates gap dynamics with a quick recover of the original forest structure values, explaining why we did not find differences between LH and control (MAT) (Tables 2–4), and they presented great similarity in the multivariate analyses (Figs. 3 and 4). Low intensity harvesting represents thinning interventions made by ranchers with a double purpose: to obtain poles for fences and lumber, and to slightly open the forest canopy to stimulate the understory growth and provide shelter for cattle mainly during winter (Peri et al., 2016a; Martínez Pastur et al., 2018). It is an example of how the effects on ecosystem services, biodiversity and resilience varied according to the management objectives, which depend on the service chosen to be prioritized or maintained over time (Peri et al., 2017). Other studies also show that thinning practices modify forest resilience, both in ñire forests of Tierra del Fuego (to face insect attacks as caterpillar outbreaks, Martínez Pastur et al., 2018), mixed ñire forests of northern Patagonia (to harvesting, Chillo et al., 2020), and other forests of the world (e.g. to drought events in southwest Germany European beech, Diaconu et al., 2017; and in relict Mediterranean forests of *Abies pinsapo*, Casas-Gómez et al., 2020).

High intensity harvesting (HH) generated great changes compared with natural dynamic in ñire forests, where large impacts are unusual due to semi-open canopies and low tree height compared to the other Fuegian forest types, such us *N. pumilio* forests (Ivancich, 2013; Gönc et al., 2015; Martínez Pastur et al., 2018). These large canopy openings promote abundant natural regeneration from seeds and root sprout (Steinke et al., 2008; Soler et al., 2013, 2018). However, regeneration can fail due to over-browsing (e.g. cattle, sheep and *Lama guanicoe*), abiotic damages (frosting and drying), or lack of overstory protection during early recruitment phases (Gea et al., 2004; Raffaele et al., 2011; Echevarría et al., 2014; Martínez Pastur et al., 2016a; Peri et al., 2017; Bahamonde et al., 2018). In our analyses, we found some differences between HH and control (MAT) (Tables 2–4), mainly due to the decreasing in magnitude of forest structure variables and the modification of some soil properties (e.g. increasing in soil bulk density) that determined a major differentiation in the multivariate analyses (Figs. 3 and 4). A similar trend but with greater magnitude was observed in the clear-cuts (CC), both for the univariate and multivariate analyses. The magnitude of the differences in the studied variables was directly related to the intensity of the cuttings.

The presence of natural regeneration in both treatments (HH and CC) allowed stand recovery in the medium-term (e.g. 20–40 years), returning the forest structure to one comparable with natural conditions (e.g. YUA or IGP forests) (Martínez Pastur et al., 2013). However, the absence of natural regeneration can lead to different pathways, such the transformation of the forest stands into grasslands (e.g. see Peri et al., 2017). The high intensity interventions leading to dieback of the remnant overstory, may also induce vulnerability to insect attacks and diseases (Navarro-Carrillo et al., 2008; Martínez Pastur et al., 2018). High intensity harvesting was applied by ranchers with the purpose to increase understory forage and provide shelter for livestock (Bahamonde et al., 2012; Peri et al., 2016a; Álvarez et al., 2020).

In the past, intentional fires were commonly used as a land conversion practice in Patagonia, implemented by ranchers since the beginning of European settlements (Gea et al., 2004; González et al., 2020), to remove forests for livestock production (Huber and Markgraf, 2003; Peri et al., 2016a). Fire generates great modifications that affected soil properties and creates a different vegetation dynamic pathway (Veblen et al., 1992). Several studies show that fires change forest structure, understory assemblage, dynamic cycles and soil in ñire forests (Armesto et al., 1992; Gönc et al., 2015; Sotomayor et al., 2016), as well as in other forests of the world (e.g. Ryan 2002; Neary et al., 2003; Wang and Kemball, 2005; Yildiz et al., 2010; Da Silva Ramos Vieira Martins et al., 2012). In Tierra del Fuego, natural fires are not considered natural drivers in the *Nothofagus* succession dynamics, since evidences show these are mainly originated by humans (Gutiérrez, 1994). To date, this practice has been forbidden, however large patches were transformed using this practice until 1970s. Fire occurrence was randomly located across the landscape (Table 1) and stand characteristics (e.g. site quality). In the harvested stands, we found some differences between burned stands and control (MAT) (Tables 2–4), mainly in the forest structure variables. However, the differences were greater than those treatments, leading to higher split in the groups of the multivariate analyses (Figs. 3 and 4). One conspicuous group was represented by large burned areas before the 1970s, heavily regenerated and converted in overstocked even-aged young stands (IGP) (e.g. Viamonte and Los Cerros ranches) (Soler et al., 2013; Martínez Pastur et al., 2013). Another group was represented by areas converted to grasslands with native or exotic species commonly used for grazing (Lencinas et al., 2008; Bahamonde et al., 2012). Usually, these great impacts allow the invasion of undesirable species that decrease the potential for livestock purposes (e.g. *Hieracium pilosella*) (Alonso et al., 2020; Martínez Pastur et al., 2020b).

The natural ñire forests occur intermixed with other associated environments (e.g. dry and humid grasslands) in landscapes. The edges between forests and openlands are not stable, and change according to climate fluctuations (Bond, 2019), e.g. forest edge regeneration can lead to new forested areas on medium and long-time (50–100 years). The environmental conditions that limit the forest advance are related to topography, soil moisture, wind exposure and extreme climate during winter (Valenzuela et al., 2016). The forest removal (e.g. CC and fires) generated conditions more similar to openlands than natural forests. However, when the regeneration had been established in the edges, the conditions get closer to forested areas (Tables 2–4, Figs. 3 and 4).

4.3. Implications for a sustainable management: What is the threshold of non-return?

Tierra del Fuego natural forests have a simple forest structure and low diverse assemblage of species, following predictable dynamic pathways, a desirable characteristic for the design of management practices (Martínez Pastur et al., 2013; Peri et al., 2016a). These forests offer diverse supply of ecosystem services: (i) the provisioning services mainly based on livestock and secondarily, on wood products (Martínez Pastur et al., 2018; Rosas et al., 2021); (ii) the great regulating and supporting services, where nutrient and water cycles allow the maintenance of several species that do not occur elsewhere (Martínez Pastur et al., 2017); and (iii) the cultural ecosystems services related to recreation (e.g. trout fishing) and tourism, being the main landscape selected by the inhabitants of northern city (e.g. Río Grande) (Martínez Pastur et al., 2016b; Rosas et al., 2021).

Sustainable management of these forests must include the maintenance of these services, and assure the stand regeneration capacity and the resilience to face unexpected natural changes (e.g. extreme climate events) (Reque et al., 2007; Peri et al., 2017). According to our results, the different forests maintained similar values in the studied parameters, however, a previous study determine that mature uneven-aged stands (MUA, Fig. 1) presents higher biodiversity values (Martínez Pastur et al., 2020b). Because managed stands had lower biodiversity values, it is necessary to identify and preserve MUA stands. These forests with higher conservation values are crucial for the species maintenance at landscape level (Hilmers et al., 2018) and ecosystem functions that maintain natural life support processes (Oliver et al., 2015).

To date, more ecological friendly management practices had been proposed for the native forests in Patagonia. Silvopastoral management generates a positive balance among provisioning services and the other ecosystem services (regulating, supporting, cultural), ecosystem functions and biodiversity conservation (Lindenmayer et al., 2006, 2012). However, according to our results, the thinning proposals must be based on light harvesting (basal area 38.78 $\pm$ 8.62 standard deviation) rather than intense interventions (basal area 17.26 $\pm$ 7.77 standard deviation) to maintain most of the natural forests values, in coincidence with findings of Nacif et al. (2020). The negative aspect of light thinning is that this requires more frequent interventions, deriving in expensive management practices (e.g. every 5 years compared with one intervention). The implementation of heaviest thinning generates deep changes in the stands, and increases the risks of permanent modifying the dynamics pathways, or at least that will require longer periods of time to recover the naturalness and the provision of non-monetary ecosystem services. Moreover, remnant canopy also quickly closes after the heavy thinning implementation (e.g. 5–7 years for 30% canopy removal), which makes more expensive this kind of harvesting too.

The adaptations to the environment allowed the ñire forests to persist on time, and must be considered for the development of better management and conservation practices. Resilience of ñire forests is closely related to the harvesting impact level that reduces the overstory values, and the modification of natural regeneration capacity. The different management practices (e.g. livestock stocking and thinning intensity) should contemplate a balance among the provisioning services and other ecosystem services (e.g. livestock comfort, recreation, aesthetic) and biodiversity (e.g. local extinction of species and invasion of exotic species). Currently, management and conservation actions are conducted through the implementation of compulsory plans that the ranch owners must present to the Regional Forest Office, according to the provincial forest regulations (law 145/94) and the territorial forest ordination (national law 26331/07). Results of our study may assist policy-makers to better define the regulations of the silvicultural practices, considering the advantages for provisioning services, but also the risks due to the modification in the natural cycles and resilience of these forests, as was also stated by Rusch et al. (2017) and Peri et al. (2017). In our analyses, harvesting intensity thresholds are important to establish desired management and conservation objectives (e.g. heavy thinnings are closer to clear-cuts and conversion landscapes, than light thinnings).

5. Conclusions

Environmental variables and natural regeneration do not greatly change across the natural dynamic cycle of ñire forests, that were modelled by different natural impacts. Forest structure changes according to the stand age, and between even- and uneven-aged stands, but these differences are lower compared to those generated by management (heavy thinnings, clear-cuts and fires). These practices largely modify the forest values, promoting changes that lead to modifications and generate more similarities with openlands. However, light thinnings allow to obtain higher provisioning services without the loss of the naturalness. The thresholds found in this study can allow to define thinning levels, and provide novel insights into the important ecological associations between ecological functions, natural regeneration and structural diversity in the ñire forests. It is necessary to consider the attributes at stand level, and to develop management strategies that improve the management planning and resilience to face climate change. Therefore, in managed forests, silvicultural systems must be able to develop or maintain forest attributes related to regeneration capacity. Much research and monitoring are still required to develop and optimize new silvopastoral proposals for a wide variety of management and conservation objectives.

CRediT authorship contribution statement

Guillermo J. Martínez Pastur: Conceptualization, Methodology, Investigation, Writing - original draft, Funding acquisition. **Yamina M. Rosas:** Investigation, Formal analysis, Conceptualization, Methodology. **Jimena Chaves:** Investigation, Formal analysis. **Juan M. Cellini:** Investigation, Data curation. **Marcelo D. Barrera:** Investigation, Writing - review & editing. **Santiago Favoretti:** Data curation, Software. **María V. Lencinas:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Funding acquisition. **Pablo L. Peri:** Writing - review & editing.

Declaration of Competing Interest

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

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