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Research article

Effectiveness of fencing and hunting to control *Lama guanicoe* browsing damage: Implications for *Nothofagus pumilio* regeneration in harvested forests

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ABSTRACT

Browsing damage by native ungulates is often to be considered one of the reasons of regeneration failure in *Nothofagus pumilio* silvicultural systems. Fencing and hunting in forests at regeneration phase have been proposed to mitigate browsing effects. This study aims to determine effectiveness of these control methods in harvested forests, evaluating browsing damage over regeneration, as well as climate-related constraints (freezing or desiccation). Forest structure and regeneration plots were established in two exclosures against native ungulates (*Lama guanicoe*) by wire fences in the Chilean portion of Tierra del Fuego island, where tree regeneration density, growth, abiotic damage and quality (multi-stems and base/stem deformation) were assessed. Exclosures did not influence regeneration density (at the initial stage with < 1.3 m high, and at the advanced stage with >1.3 m high). However, sapling height at 10-years old was significantly lower outside (40–50 cm high) than inside exclosures (80–100 cm), and also increased their annual height growth, probably as a hunting effect. Likewise, quality was better inside exclosures. Alongside browsing, abiotic conditions negatively influenced sapling quality in the regeneration phase (20%–28% of all seedlings), but greatly to taller plants (as those from inside exclosure). This highlights the importance of considering climatic factors when analysing browsing effects. For best results, control of guanaco in recently harvested areas by fencing should be applied in combination with a reduction of guanaco density through continuous hunting. The benefits of mitigation actions (fencing and hunting) on regeneration growth may shorten the regeneration phase period in shelterwood cutting forests (30–50% less time), but incremental costs must be analysed in the framework of management planning by means of long-term studies.

1. Introduction

Guanacos (*Lama guanicoe*) are the only large native herbivores on Tierra del Fuego island (Bonino and Fernández, 1994; Cavieres and Fajardo, 2005; Baldi et al., 2010). They are generalist species, which inhabits a large variety of environments, from arid steppe to subalpine grasslands, deciduous and evergreen forests (Bahamonde et al., 1986; Puig et al., 1997; Rebertus et al., 1997; Baldi et al., 2010), and they includes many plants in its diet, from young trees to epiphytes (Soler Esteban et al., 2012, 2013; Muñoz and Simonetti, 2013). Guanacos were an essential subsistence resource for hunter-gatherer societies from the earliest occupations around 10,000 years ago (Borrero, 1999), and abundant archaeological information indicates that they used *Nothofagus* forests during the last 6400 years until arrival of European people (Gusinde, 1931; Orquera and Piana, 1999; Tivoli and Zangrando, 2011). These facts show that guanacos and *Nothofagus* forests have coexisted and co-evolved for thousands of years. Some authors suggest that high stocking rates of sheep (*Ovis aries*)

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introduced by Europeans in Tierra del Fuego reduce forage availability to guanacos, promoting over-use of forests (Raedake, 1982; Muñoz and Simonetti, 2013; Moraga et al., 2015) and therefore affecting natural regeneration dynamics of the latter (Pulido et al., 2000; Cavieres and Fajardo, 2005). However, some authors affirm that sheep did not displace guanacos, and both can coexist in the same area (Iranzo et al., 2013).

Current silvicultural prescriptions for commercial harvesting of lenga (*Nothofagus pumilio*) forests are mainly based on canopy openings that stimulates natural regeneration by modifying soil moisture and light availability at ground level (Martínez Pastur et al., 2014). The most widespread silvicultural method applied to lenga in Southern Chile is shelterwood cutting (Rosenfeld et al., 2006). Abundant establishment and fast growth of seedling occur after cuts (Martínez Pastur et al., 2011a), but tree regeneration during the regeneration phase is highly vulnerable to climate-related damage (freezing or desiccation) (Martínez Pastur et al., 2011b), competition with understory plants (Martínez Pastur et al., 2014; Henn et al., 2014) and browsing by guanacos and domestic herbivores (Soler Esteban et al., 2012; 2013). Synergistic effects among these risk factors may occur, with the added problem of tree blown down by severe wind storms (Rebertus et al., 1997).

Browsing by guanaco is identified as one potential cause for silviculture failure at large scale (Pulido et al., 2000). To counteract this, different initiatives have been proposed and implemented to control them. In Chilean forests of Tierra del Fuego, two strategies are used, as in other temperate forests (e.g. Beguin et al., 2009): (i) exclosures by wire fencing of forests at the regeneration phase, and (ii) hunting to reduce guanaco population. However, there are not quantitative results to demonstrate the effectiveness of these control strategies to diminish the guanaco's browsing impact on lenga forests. Therefore, the aim of this work was to determine the effects of fencing and hunting over natural regeneration of harvested lenga forests. The following questions were addressed: (i) do exclosures influence density, quality and growth of seedlings in the initial stage of regeneration in harvested forests (<1.3 m height)?; (ii) do exclosures influence density and quality of saplings in the advanced stage of regeneration in harvested forests (>1.3 m height)?; (iii) does hunting reduce browsing damage and improve regeneration growth?; and (iv) what is the magnitude of climate-related injuries (freezing or desiccation) compared to browsing damage?

2. Materials and methods

2.1. Study site

Lenga forests naturally regenerate by wind-dispersed seeds. Seedlings are mid shade-tolerant. They can survive under closed canopy in the understory strata for long periods of time (up to 10 years). However, the seedlings greatly increase height growth under open canopies (Martínez Pastur et al., 2007), as those environmental conditions generated by harvesting. Silvicultural methods for these forests in southern Patagonia include long regeneration periods (15–20 years), which are followed by several thinning interventions before the end of the forest management cycle (70–100 years) (Rosenfeld et al., 2006; Martínez Pastur et al., 2009).

The study area (aprox. 1000 ha) was located in a pure lenga forest on Tierra del Fuego Island (Chile) (53°40′ to 53°45′ S, 69°08′ to 69°10′ W), where a private company harvested primary forests through shelterwood cuttings (Martínez Pastur et al., 2009). Shelterwood cuttings are usually carried out in two stages: (i) a first cut, which leaves dominant trees (30–40 m^2 ha^{-1} basal area) evenly distributed in the harvested area to stimulate the natural regeneration establishment and growth under an open canopy, and (ii) a final cut, which removes all remnant trees after regeneration reaches 1.3 m height and successfully covers most of the harvested area. The climate is characterized by short, cool summers and long, snowy winters with frequent occurrence of frosts. Only three months per year have daily temperatures above 0 °C, and the growing season extends approximately five months (November to March). Rainfall, including snowfall, reaches up to 600 mm yr^{-1}. Annual wind speed outside forests is 8 km h^{-1} in average, reaching up to 100 km h^{-1} during storms (Martínez Pastur et al., 2009).

2.2. Guanaco natural population and hunting

On Chilean Tierra del Fuego, the guanaco population collapsed by mid-1970s as a result of hunting, competition with sheep and habitat degradation, declining to 7000 individuals (Moraga et al., 2015). However, in the following years, guanaco population greatly increased (× 8), reaching approximately 57,000 individuals in 2011 (Skewes Ramm and Aravena Bustos, 2011). For this reason the Chilean government authorized some companies to hunt guanacos, to reduce browsing and damage on harvested forests and to sell their meat (Moraga et al., 2015). During 2010–2011, 4500 adult individuals were hunted in the steppe-forest ecotone (Skewes Ramm and Aravena Bustos, 2011), in which the study area is included, where density was estimated in 2.1 ind km^{-2} (Montes et al., 2000). It must be considered that Tierra del Fuego is shared between Chile and Argentina, and guanaco range freely all over the island.

2.3. Fencing treatments

Two guanaco exclosures (AREA 1 and AREA 2) delimited by wire fences of 2.25 m high were analysed in this study (Annex 1A). Fences were constructed by 14 horizontal wires with a barbed wire in the top, and wooden poles every 1 m. Exclosures were established in two sites harvested by the first cut of a shelterwood cutting but with a different later history. AREA 1 was harvested in 1994; however remnant structure was affected by a wind storm in 1998 that blown down almost all trees in the area, so the forest operator also extracted the timber logs of the fallen trees. AREA 2 was initially harvested in 1990, and final cut was applied in 2004. Both sites were considered especially sensitive and threatened by guanaco browsing by the forest operator, therefore fences were established in 2002 in AREA 1 (260 ha), and in 2006 in AREA 2 (9 ha). At the time of this study (December 2011), regeneration was at the initial stage (< 1.3 m high) in AREA 1, and at the advanced stage (> 1.3 m high) in AREA 2. In both sites, outside exclosure situations were analyzed near fenced areas, which had identical history and similar climate conditions to inside exclosure situations.

2.4. Forest structure and regeneration measurements

Sampling was conducted at the beginning of the growing season. Plot layout was organized in sections along fences (Annex 1B), with a paired sampling design inside and outside exclosures. In AREA 1, four sections were surveyed, with 20 plots each (10 inside and 10 outside exclosure), totalizing 80 plots (4 × 10 × 2). In AREA 2, six sections were surveyed, with 6–8 plots each (3–4 inside and 3–4 outside exclosure), totalizing 40 plots (6 × 3–4 × 2). Length and width of each plot were variable in size, to include enough area until compulsory count 20 seedlings or saplings (> 3 years old).

Remnant forest structure in AREA 1 was characterized at each plot by angle count sampling, following Bitterlich (1984) and using a Criterion RD-1000 (Laser Technology, USA) with a variable basal area factor (K) between 1 and 6, which allowed to recording tree basal area (BA) and density (TD). Also, dominant height (DH) and DBH of remnant structure were measured. Complementarily, ground cover were estimated in both AREA 1 and AREA 2 as by point intercept method in each plot, using 100 interception points, and analysing woody debris cover by size, as big (>30 cm diameter), medium (5–30 cm) and fine (< 5 cm), or cover without debris (bare soil, regeneration and/or understory plants).

For each seedling the following data was recorded: (i) regeneration density (RD), calculated dividing 20 plants for the area of each plot; (ii) total height (H), measured from the base to the top of the longest shoot; (iii) quality, including the presence of multistems (MS) or deformations in base (DB) or stem (DS), which was defined as a lack of straight stem that can be related to old browsing or climate-related damage; (iv) browsing damage (BD), observed in the sprouts during the last growing season (2010–2011); (v) climate-related injuries as freezing or desiccation (FDI), observed in the sprouts during the last growing season (2010–2011), which was identified as dead sprouts. In AREA 2, mean diameter at breast height (DBHr) was also measured when plants exceeded 1.3 m height, and corresponding basal area (BAr) was calculated using the area of each plot. Likewise, one sapling of average size was collected for stem analysis in each plot. To estimate age, tree rings were measured every 10 cm in AREA 1, and every 20 cm in AREA 2, from the base to the top of the longest shoot, and height growth was calculated using height-age data pairs. Additionally, annual apical growth of seedlings was estimated in AREA 1 for the last four years (2008–2011), classified as before (2008–2009) and after (2010–2011) hunting, and also difference between periods (DIF) was calculated.

2.5. Statistical analyses

Multiple analyses of variance (ANOVA) were performed considering sections (four levels in AREA 1 and six levels in AREA 2) and exclosures (two levels, inside and outside, in both AREA 1 and AREA 2) as main factors. In AREA 1, the analyzed response variables were: (i) forest structure (BA, DH, TD, DBH); (ii) ground cover; (iii) regeneration metrics (H, RD); (iv) regeneration quality (MS, DB, DS) and damage (BD, FDI); and (v) regeneration annual growth (before and after hunting). In AREA 2, response variables were: (i) ground cover; (ii) regeneration metrics (DBHr, H, RD, BAr); and (iii) regeneration quality (MS, DB, DS). In all tests means were compared by Tukey test ($p < 0.05$). For height growth, r^2 of the linear tendency for age-height pairs was compared among sections, and inside and outside exclosures.

Complementarily, two principal component analyses (PCA) were conducted to describe the general structure of the regeneration, including the following variables: regeneration annual growth before (BEFORE) and after (AFTER) hunting, regeneration metrics (H, RD), regeneration quality (MS, DB, DS) and climate-related damage (BD, FDI) for AREA 1; and regeneration metrics (DBHr, H, RD, BAr) and quality (MS, DB, DS) for AREA 2. PCA analysis included Monte Carlo permutation test ($n = 999$) to assess the significance of each axes. Differences between inside and outside exclosures were assessed using a multi-response permutation procedure (MRPP), a non-parametric method that tests for multivariate differences among a priori defined treatment groupings. PCA and MRPP tests were conducted in PCORD version 4.01 (McCune and Mefford, 1999).

3. Results

3.1. Fencing effect on initial regeneration stage of harvested forests (AREA 1)

Marginal differences in remnant forest structure were detected inside and outside exclosure. There were higher basal area and tree density (2.2 m^2 ha^{-1} and 9 trees ha^{-1}) inside than outside exclosure (1.2 m^2 ha^{-1} and 5 trees ha^{-1}). However, this remnant basal area only represented 6.3% and 3.4% of the basal area left after the first shelterwood cut. Wind storm greatly affected south-west aspects and high altitudes, which explain heterogeneity among sections, where areas with bigger DBH trees were more resistant to wind than areas with lower DBH (Table 1). Woody debris cover generated by fallen trees or left by harvesting did not significantly vary inside or outside exclosure, or among sections. Ground cover in AREA 1 corresponded to 32% of woody debris (55% big, 29% medium, and 16% fine) and 68% of other covers (bare soil, regeneration and/or understory plants) without debris (Annex 2).

Regeneration density did not significantly vary between inside and outside exclosure (26 and 41 thousand ha^{-1}, respectively), neither among sections. However, significant differences were found for height inside and outside exclosure (106.4 cm compared to 43.3 cm, respectively) and among sections (60.5 cm–85.3 cm) (Table 2). Regeneration quality did not vary among sections, but significantly varied with exclosure. Multi-stems and deformation in base and stem were more common outside (23%, 55% and 36% of saplings, respectively) than inside exclosure (8%, 24% and 14% of saplings, respectively) (Table 3).

The stem analyses also showed the same trend, whit higher height growth inside than outside exclosure (Fig. 1) in the four sections. Height growth increased in time in both sectors, inside (r^2 of 0.49, 0.71, 0.56 and 0.52 for the four sections) and outside exclosure (r^2 of 0.45, 0.58, 0.60 and 0.64 for the four sections). The difference between both trend lines represented a delay of seedling growth of 12 years for Section 1, 10 years for Section 2, 8 years for Section 3, and 7 years for Section 4. This delay can be interpreted as additional years necessary for plants outside exclosure to reach similar heights than inside exclosure, and can be understood as an indicator of the benefit of fence construction.

PCA ordination allowed us to compare plots inside and outside exclosure, and it is possible to detect that the two groups slightly overlapped (Fig. 2). Eigenvalues for the first two axes were 4.264 ($p = 0.001$) and 1.463 ($p = 0.056$), explaining 47.4% and 63.6% accumulative variation of the total dataset. The factors with the highest absolute coefficient for Axis 1 were: H > BD > BEFORE > DB; and those for Axis 2 were: RD > DS > DB > MS. Quantitative variables that define inside exclosure treatment were related to plant growth and climate injuries, while variables that define outside exclosure treatment were related to plant quality and browsing damage. MRPP analysis detected significant differences between both treatments ($T = -35.09$, $A = 0.2556$, $p < 0.01$), indicating that centroid position of each treatment significantly differed between them in the ordination space of the studied variables.

3.2. Fencing effect on advanced regeneration stage of harvested forests (AREA 2)

The woody debris cover from occasional windthrow or material left after harvesting did not significantly vary inside or outside exclosure, or along the different sections (Annex 3). While 75% of the area corresponded to other covers (bare soil, regeneration and/or understory plants) without debris, 25% of forest floor was occupied by woody debris (57% big, 32% medium, and 11% fine). There were no differences in regeneration variables among sections

Table 1
Multiple ANOVA for forest structure (average ± standard deviation) in AREA 1 with section (1–4) and exclosure (inside and outside) as main factors, analysing tree basal area (BA) (m^2 ha^{-1}), density (TD) (n ha^{-1}), dominant height (DH) (m) and mean diameter at breast height (DBH) (cm).

Main factors		BA	TD	DH	DBH
Section	1	0.7 ± 0.9 a	7.3 ± 9.5	18.3 ± 1.0	34.7 ± 4.7 a
	2	3.3 ± 3.7 b	8.4 ± 10.8	18.8 ± 1.0	71.7 ± 13.7 b
	3	1.8 ± 1.5 ab	5.8 ± 5.9	18.5 ± 1.1	67.4 ± 14.2 b
	4	1.2 ± 1.9 a	5.6 ± 9.4	19.0 ± 1.2	59.5 ± 12.5 b
	$F_{3,72}(p)$	*5.62(0.002)*	*0.44(0.728)*	*1.96(0.127)*	*17.7(<0.001)*
Exclosure	inside	2.2 ± 3.0 b	8.9 ± 10.3 b	18.6 ± 1.1	55.2 ± 19.2
	outside	1.2 ± 1.6 a	4.6 ± 6.9 a	18.7 ± 1.1	61.4 ± 17.2
	$F_{1,72}(p)$	*4.50(0.037)*	*4.81(0.031)*	*0.73(0.396)*	*2.39(0.130)*
Interaction	$F_{3,72}(p)$	*2.76(0.048)*	*1.26(0.296)*	*6.67(0.001)*	*1.80(0.162)*

$F_{s,r}(p)$ = Fisher test and significance between brackets, with “s” and “r” as degrees of freedom. Different letters indicate significant differences at p < 0.05 using Tukey test.

Table 2
Multiple ANOVA for regeneration metrics (average ± standard deviation) in AREA 1 with section (1–4) and presence (inside and outside) as main factors, analysing height (H) (cm) and density (RD) (thousand ha^{-1}).

Main factors		RD	H
Section	1	29.3 ± 45.2	85.3 ± 38.8 b
	2	28.2 ± 18.8	69.5 ± 38.5 a
	3	42.2 ± 45.1	60.5 ± 39.0 a
	4	34.5 ± 27.5	84.0 ± 28.5 b
	$F_{3,72}(p)$	*0.62(0.601)*	*10.74 (<0.001)*
Exclosure	inside	26.4 ± 27.4	106.4 ± 19.6 b
	outside	40.6 ± 41.6	43.3 ± 19.3 a
	$F_{1,72}(p)$	*3.14(0.080)*	*300.19 (<0.001)*
Interaction	$F_{3,72}$ (p)	*0.34(0.798)*	*2.81(0.045)*

$F_{s,r}(p)$ = Fisher test and significance between brackets, with “s” and “r” as degrees of freedom. Different letters indicate significant differences at p < 0.05 using Tukey test.

Table 3
Multiple ANOVA for regeneration quality and damage (average ± standard deviation) in AREA 1 with section (1–4) and exclosure (inside and outside) as main factors, analysing multi-stem plants (MS) (%), deformation in base (DB) (%) and stem (DS) (%), browsing damage (BD) (%) and freezing or dessication injuries (FDI) (%).

Main factors		MS	DB	DS	BD	FDI
Section	1	13.7 ± 2.8	41.2 ± 27.8	19.5 ± 21.5	53.8 ± 34.3	23.0 ± 12.7
	2	17.0 ± 3.4	42.2 ± 30.0	21.2 ± 17.8	55.0 ± 43.1	20.2 ± 12.1
	3	18.0 ± 3.6	43.0 ± 19.8	28.0 ± 13.6	59.2 ± 42.1	22.5 ± 14.3
	4	12.7 ± 2.6	31.5 ± 20.7	29.8 ± 19.1	56.5 ± 37.0	28.0 ± 24.3
	$F_{3,72}(p)$	*0.92(0.433)*	*1.59(0.198)*	*2.39(0.075)*	*0.22(0.880)*	*0.84(0.477)*
Exclosure	inside	8.0 ± 3.2 a	24.1 ± 17.9 a	13.5 ± 9.3 a	31.1 ± 31.1 a	29.1 ± 18.6 b
	outside	22.8 ± 9.1 b	54.8 ± 21.3 b	35.8 ± 18.6 b	81.1 ± 27.6 b	17.7 ± 11.9 a
	$F_{1,72}(p)$	*31.65(<0.001)*	*52.03(<0.001)*	*47.20(<0.001)*	*99.59(<0.001)*	*10.15(0.002)*
Interaction	$F_{3,72}(p)$	*1.95(0.128)*	*2.07(0.111)*	*0.44(0.726)*	*26.69(<0.001)*	*0.06(0.979)*

$F_{s,r}(p)$ = Fisher test and significance between brackets, with “s” and “r” as degrees of freedom. Different letters indicate significant differences at p < 0.05 using Tukey test.

(Table 4). Also, height (3.2–3.3 m), density (20.8–21.7 thousand ha^{-1}), diameter (1.7–1.8 cm) and basal area (10.3–11.5 m^2 ha^{-1}) did not significantly vary between exclosure treatments. However, presence of multi-stems was significantly higher outside (8.4%) than inside (3.0%) exclosure (Table 5), although the exclosure did not determine differences on sapling deformation at the base (14%–20%) or along the stem (24%–27%).

The stem analyses showed similar trends in both treatments, where height growth inside and outside exclosure did not greatly vary (Fig. 3). However, during early stages of growth (0–1 m high), growth trend line showed major changes between inside and outside exclosure, compared to treatments at later stages growth (1–2 m high). Moreover, it was possible to observe that growth rate at later stages was 2 times higher than rate at early stages.

PCA ordination did not reflect a clear separation between exclosure treatments, due to outside plots presented great dispersion (Fig. 4). Eigenvalues for the first two axes were 2.950 (p = 0.001) and 1.371 (p = 0.398), explaining 42.1% and 61.7% of the accumulated variation of the total dataset. The factors with the highest absolute coefficient for Axis 1 were: Bar > DBHr > H > RD; and those for Axis 2 were: DB > MS > RD > DS. In this analysis, it was not possible to define quantitative variables for each exclosure treatment. However, two variables of plant quality (MS and DB) explain the major variation of outside exclosure treatment. MRPP analysis did not show significant differences between both treatments (T = 1.16, A = −0.0180, p = 1.00), indicating that centroid position of each treatment did not significantly differ between them in the ordination space of the studied variables.

3.3. Effectiveness of guanaco hunting on seedlings growth (AREA 1)

Comparisons of annual height growth for before and after hunting (Table 6) showed, as it was expected, height growth was significantly higher (9.0 to 9.8 cm $year^{-1}$, before and after hunting respectively) inside than outside exclosure (5.3–6.4 cm $year^{-1}$, respectively). Inside exclosure, a slight decrease in the growth rate was detected (−0.8), probably due to climatic events, but outside exclosure the average growth increased 1.1 cm $year^{-1}$. This increment represented an improvement of 20.7% compared to the initial growth. However, differences within sections were found probably

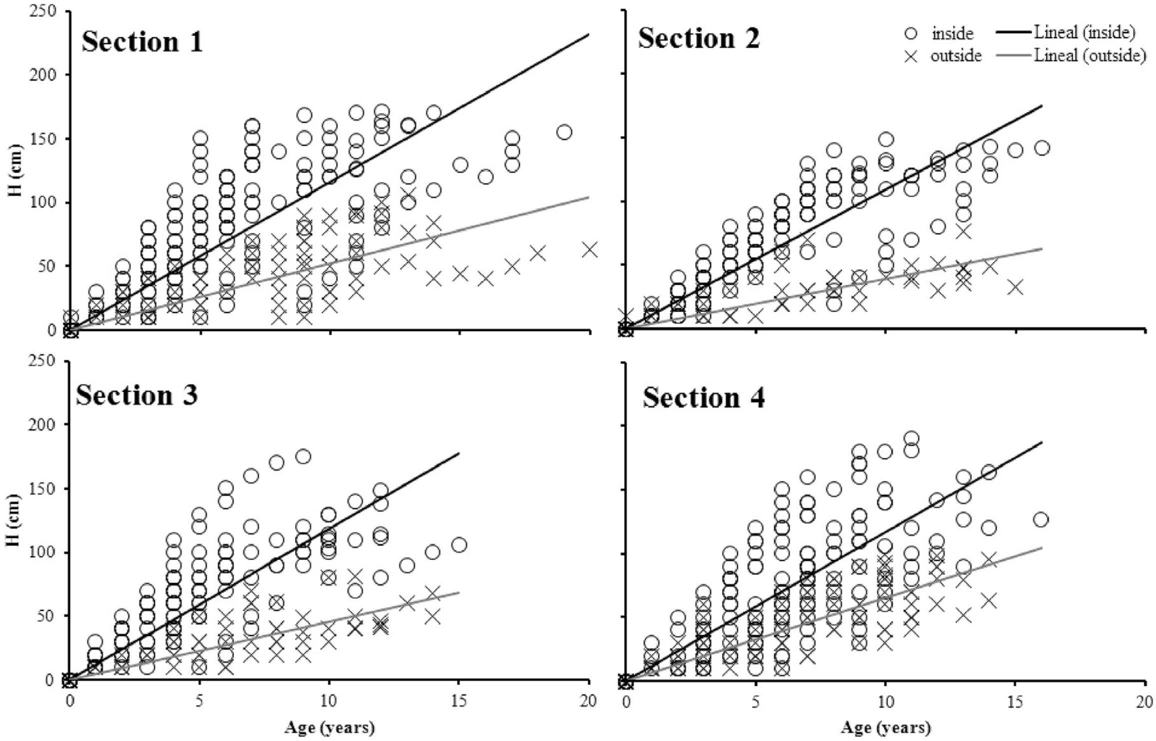


Fig. 1. Stem analysis of saplings from sections of the AREA 1, considering age-height (H) pairs inside and outside exclosure. Tendency lines for each inside and outside exclosure were included.

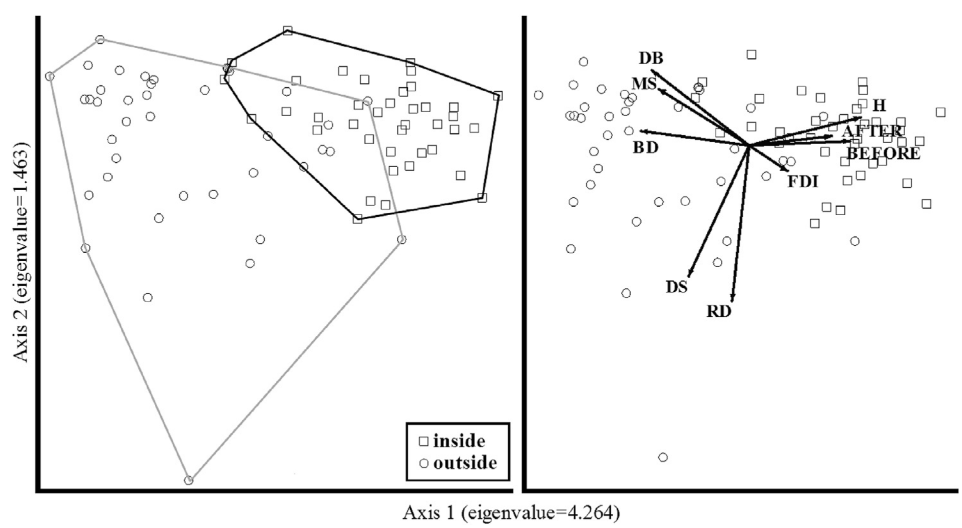


Fig. 2. Principal component analysis (PCA) ordination for regeneration plots of AREA 1 classified by inside and outside exclosure, including the following variables: H = height (cm), RD = regeneration density (thousand.ha^{-1}), MS = multi-stems (%), DB = deformation in base (%), DS = deformation in stem (%), BD = browsing damage (%), FDI = plants with freezing or dryness injuries (%), BEFORE = annual growth before hunting (cm year^{-1}) and AFTER = annual growth after hunting (cm year^{-1}).

due to inherent conditions of stands (site quality or shelter influence of remnant basal area). One section presented greater growth after hunting (increments of 2.2 cm year^{-1}), but the others presented lower growths (−0.4 to −0.9 cm year^{-1}).

3.4. Impact of climate-related injuries compared to browsing damage

Browsing damage and freezing or desiccation injuries on seedlings did not significantly vary among sections in AREA 1. However, these damages significantly varied with exclosure (Table 3). Outside exclosure 81% of seedlings showed browsing damage, while inside exclosure 31% had browsed sprouts. Some guanacos forage inside the exclosures, at least during the studied growing season, due to the presence of some browsed plants were detected during samplings. On the other hand, freezing or desiccation injuries were significantly higher inside exclosure (29%) where plants were taller (106 cm high), than outside exclosure (18% damage in seedlings 41 cm high in average).

Table 4
Multiple ANOVA for regeneration metrics (average ± standard deviation) in AREA 2 with section (1–6) and exclosure (inside and outside) as main factors, analysing mean diameter (DBHr) (cm), height (H) (m), density (RD) (thousand ha^{-1}) and basal area (BAr) (m^2 ha^{-1}) of the advanced regeneration.

Main factors		H	RD	DBHr	BAr
Section	1	3.9 ± 1.3	15.9 ± 8.4	2.5 ± 1.2	16.2 ± 14.4
	2	3.5 ± 0.6	31.2 ± 11.4	2.0 ± 0.4	15.9 ± 3.1
	3	3.0 ± 0.8	21.4 ± 18.1	1.6 ± 0.8	10.5 ± 14.8
	4	3.2 ± 0.8	23.6 ± 16.0	1.8 ± 0.7	12.8 ± 12.2
	5	3.0 ± 0.9	16.9 ± 9.8	1.3 ± 0.5	6.0 ± 5.0
	6	2.9 ± 0.7	18.4 ± 12.2	1.1 ± 0.8	4.0 ± 5.3
	$F_{5,28}(p)$	*0.93(0.475)*	*1.19(0.337)*	*2.36(0.066)*	*1.24(0.318)*
Exclosure	inside	3.3 ± 0.8	21.7 ± 13.6	1.8 ± 1.0	11.5 ± 12.3
	outside	3.2 ± 1.0	20.8 ± 13.7	1.7 ± 0.8	10.3 ± 9.8
	$F_{1,28}(p)$	*0.05(0.831)*	*0.05(0.827)*	*0.18(0.673)*	*0.11(0.745)*
Interaction	$F_{5,28}(p)$	*0.27(0.927)*	*1.68(0.172)*	*0.53(0.750)*	*0.43(0.822)*

$F_{s,r}(p)$ = Fisher test and significance between brackets, with "s" and "r" as degrees of freedom. Different letters indicate significant differences at p < 0.05 using Tukey test.

Table 5
Multiple ANOVA for regeneration quality (average ± standard deviation) in AREA 2 with section (1–6) and exclosure (inside and outside) as main factors, analysing multi-stem (MS) (%) and deformation in base (DB) (%) and stem (DS) (%).

Main factors		MS	DB	DS
Section	1	6.4 ± 10.9	18.5 ± 4.8	33.7 ± 6.9
	2	7.5 ± 9.3	17.5 ± 7.6	21.7 ± 12.1
	3	3.9 ± 5.3	21.7 ± 2.9	30.0 ± 13.1
	4	2.5 ± 2.7	10.6 ± 6.2	20.6 ± 14.2
	5	10.8 ± 12.0	19.2 ± 5.8	20.0 ± 8.4
	6	3.3 ± 4.0	12.5 ± 4.2	25.0 ± 14.4
	$F_{5,28}(p)$	*1.05(0.408)*	*0.80(0.560)*	*1.65(0.178)*
Exclosure	inside	3.0 ± 3.4 a	13.6 ± 6.7	26.6 ± 11.6
	outside	8.4 ± 10.3 b	19.7 ± 16.8	23.7 ± 13.0
	$F_{1,28}(p)$	*4.77(0.037)*	*2.31(0.139)*	*0.62(0.438)*
Interaction	$F_{5,28}(p)$	*0.77(0.577)*	*1.29(0.294)*	*1.86(0.133)*

$F_{s,r}(p)$ = Fisher test and significance between brackets, with "s" and "r" as degrees of freedom. Different letters indicate significant differences at p < 0.05 using Tukey test.

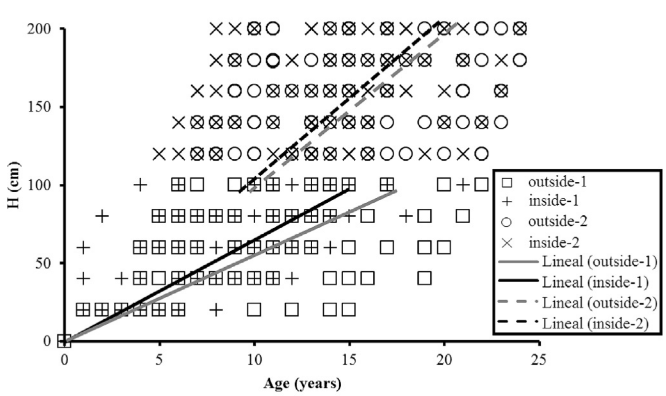


Fig. 3. Stem analysis of saplings of the AREA 2, considering age-height (H) pairs inside and outside exclosure height stem section and the fence protection. With-1 = stem analysis for 0–100 cm height inside the fences; without-1 = stem analysis for 0–100 cm height outside the fences; with-2 = stem analysis for 0–200 cm height inside the fences; without-2 = stem analysis for 0–200 cm height outside the fences. Tendency lines for each group were included.

4. Discussion

This work analysed the effectiveness of fencing and hunting to control guanaco populations and therefore, browsing damage and the implications for *N. pumilio* regeneration in harvested forests. One of the weakness of the applied methodology can be related to the lack of quantification of damage inducing factors, such as: (i) quantification and changes in guanaco density during the studied period, and (ii) characterization of microclimate that can provoke freezing or desiccation. Further studies must correlate results presented here with these biotic and abiotic variables. Analyses presented here allow some potential advantages to be determined and benefits of both proposals: fencing and hunting.

4.1. Guanaco foraging in lenga forests

Guanacos include lenga shoots in their diet during the whole year, but increase the use of harvested and primary forests during summer and spring (Soler Esteban et al., 2012, 2013). In our study, 81% of lenga regeneration had browsing damage outside exclosures, declining quality in more than 60% of the plants. However, we did not observe differences in regeneration density. This is consistent with Cavieres and Fajardo (2005) who report similar percentages of browsing damage (89%) inside gaps of primary forests with no relationship between seedling density and guanaco abundance. Pulido et al. (2000) found greater damage in primary forests (96%) compared to harvested forests (70% in shelterwood cuttings and 61% in selective cuts) leading to losses of height growth between 46% and 50%. Although our results demonstrated a significant delay for height growth in damaged regeneration, we did not detect a cessation of growth as stated by other authors (Pulido et al., 2000). In contrast, in temperate and boreal forests other species of large herbivores modify understory, seedling density and tree composition (Heikkilä and Harkönen, 1996; Edenius et al., 2002; Relva et al., 2009; Beguin et al., 2009; Kribel et al., 2011). Since here we worked mostly in pure monospecific forests, guanaco presence did not influence the proportion of tree species in understory.

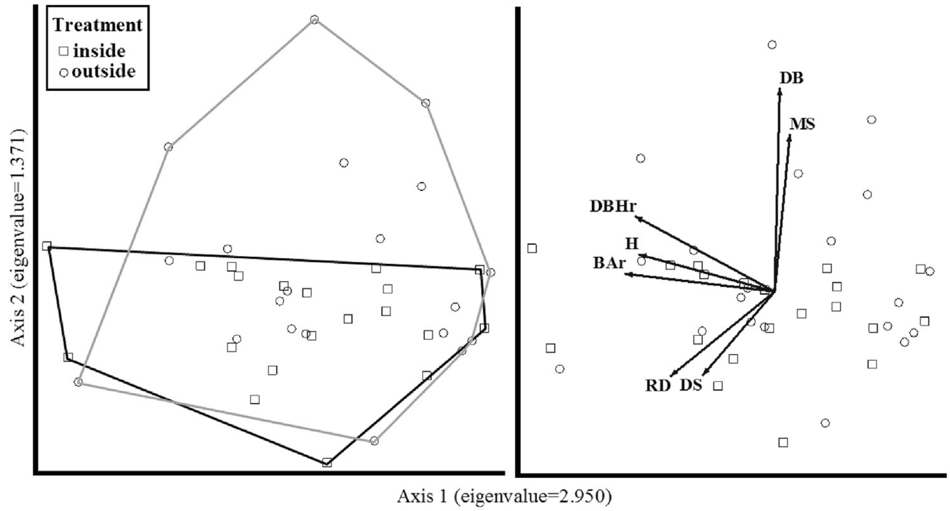


Fig. 4. Principal Component Analysis (PCA) ordination for regeneration plots of AREA 2, classified by inside and outside exclosure, including the following quantitative variables: H = plant height (cm), RD = regeneration density (thousand ha^{-1}), MS = multi-stem plants (%), DB = plants with deformation in the base (%), DS = plants with deformation along the stem (%), DBHr = mean diameter at breast height (cm), and BAr = basal area of the advanced regeneration (m^2 ha^{-1}).

Table 6
Multiple ANOVA for regeneration annual growth (average ± standard deviation) in AREA 1 with section (1–4) and exclosure (inside and outside) as main factors, analysing before (cm year^{-1}) and after (cm year^{-1}) hunting, as well as difference between periods (DIF) (cm).

Main factors		BEFORE	AFTER	DIF
Section	1	7.2 ± 2.8 ab	9.4 ± 2.7 b	2.2 ± 3.1 b
	2	7.1 ± 4.2 ab	6.7 ± 4.5 a	−0.4 ± 3.1 ab
	3	6.6 ± 4.6 a	6.3 ± 4.6 a	−0.4 ± 3.0 ab
	4	9.4 ± 3.5 b	8.5 ± 5.0 ab	−0.9 ± 5.9 a
	$F_{3,72}(p)$	*3.79(0.014)*	*4.51(0.006)*	*3.15(0.030)*
Exclosure	inside	9.8 ± 3.3 b	9.0 ± 3.7 b	−0.8 ± 4.1 a
	outside	5.3 ± 3.1 a	6.4 ± 4.7 a	1.1 ± 3.8 b
	$F_{1,72}(p)$	*49.12(<0.001)*	*14.92(<0.001)*	*5.73(0.019)*
Interaction	$F_{3,72}(p)$	*4.12(0.009)*	*20.11(<0.001)*	*6.16(0.001)*

$F_{s,r}(p)$ = Fisher test and significance between brackets, with “s” and “r” as degrees of freedom. Different letters indicate significant differences at $p < 0.05$ using Tukey test.

4.2. Fencing effectiveness

The construction of fences (Hester et al., 2000; Beguin et al., 2009) is related to a significant investment of money and effort at the beginning of the forest management cycle. Additionally, maintenance costs must be considered during the entire regeneration period. Fences need to be monitored and restored throughout the year. Natural disturbances such as individual tree blown down can cause rupture of wires and poles, which enable guanaco entrance inside exclosures (the guanaco entrance rate was estimated in <10 ind km^2 year^{-1}, unpublished data) producing damage of 31% seedlings in the fenced areas. Incremental costs to eliminate guanacos inside exclosures must also be considered in the maintenance costs. These economic valuations need further studies to analyse the feasibility of the implementation in a long-term management.

There was no evidence that fencing influence regeneration density, therefore establishment and plant survival at initial and advanced stages do not change with fencing, but this significantly affected the annual height growth and plant quality during initial growth stages. Guanaco damage limited height growth, until trees became too high to be browsed by guanacos (1.5–2.0 m) (Frelich, 2002). This explain why differences were found at initial regeneration stage between inside and outside exclosures (AREA 1), but not at advanced regeneration stage (AREA 2), both in growth and quality, and also were shown in both PCA analyses. However, further studies should analyze other factors that could affect regeneration and browsing, as differences in exclosure size (e.g., 260 ha in AREA 1 vs. 9 ha in AREA 2), management history and blown down impacts.

In forestry terms, success of fencing can be evaluated through height growth increment inside exclosures compared with outside exclosures. Also, years necessary for young trees to grow enough to escape from guanaco browsing must be considered. In harvested forests with regeneration at initial stage (AREA 1), fencing allowed plants to reach similar heights 7–12 years faster inside than outside exclosure, and with a lower percentage of stem damage. Meanwhile, in harvested forests with regeneration at advanced stage (AREA 2), growth differences were not observed, and quality differences decreased between exclosure treatments. Further studies must analyse the real benefits of these increment in height growth.

4.3. Hunting effectiveness

Hunting programmes have been proposed in different forest ecosystems as another solution to control native herbivore populations and to facilitate the recovery of vegetation communities (Beguin et al., 2009; Jenkins et al., 2014). The Chilean government has authorized six harvests of guanacos in southern Tierra del Fuego since 2004, with a total of c 14,700 harvested individuals

(Moraga et al., 2015). Thus, hunting decreases the quantity of adult guanacos in regenerating forests, but youngest groups of guanacos remain intact. This may influence geographical distribution of guanaco family groups, or change the migration pattern on the island. Besides this, young remnant individuals quickly recover family groups in controlled areas, making new control efforts necessary. It is likely that hunting has to be kept continuously at high levels to allow undisturbed growth of plants in intensive silvicultural managed forests.

Hunting allowed average height increase of seedlings (5.3 cm $year^{-1}$ vs. 6.4 cm $year^{-1}$, before and after hunting respectively), but did not show any effect on browsing outside exclosures. Moraga et al. (2015) suggest that hunting may not necessarily favour a reduction of forest browsing by guanaco, e.g. hunting guanacos during winter in forest-grassland mosaic may not be targeting guanacos that will feed in logging areas during the following summer season. Further studies must analyse the feasibility to implement these control in a long-term management at landscape level (e.g. see Baldi et al., 2010).

4.4. Climate-related injuries vs. browsing damage

During the short summer season, *Nothofagus* seedlings are vulnerable to climate-related damage, both due to desiccation (mainly during January) and freezing (mainly at the beginning and the end of growing season) (Martínez Pastur et al., 2011b). Climate-related damage kills the apical shoot and induces similar quality losses as those caused by browsing. Previous studies carried out analysing damage by guanacos in *Nothofagus* regeneration (e.g., Pulido et al., 2000) overestimated the impact of herbivores by failing to distinguish between browsing damage and climate induced damage. The percentage of freezing or desiccation injuries varied year to year depending on climatic events, e.g. ENSO (Curran et al., 1999). In our study, 20%–28% of plants presented climatic damage, and this increased inside exclosures because plants were higher and shoots presented higher individual growths, being more vulnerable to extreme climate conditions. These results showed that, browsing is not the only factor responsible for the loss of plant quality during establishment regeneration stage of harvested *Nothofagus* stands, and also insects, pest and diseases that cause similar problems. Further studies must quantify browsing and climate-related injuries in long-term forest plots, to separate and define the real impact or synergies of both types of damages.

4.5. Guanaco natural populations, sustainable forest management and regeneration dynamics

Previous studies that analysed height growth by stem analysis in *Nothofagus* forests of Tierra del Fuego (e.g. Martínez Pastur et al., 1997; Ivancich et al., 2011) show great growth variability in trees below 1.3 m height. This natural variability indicates different height growth limitations to plants during establishment regeneration stage, before plants arrive up to 1.5–2.0 m. For some tree species, this variability can be due to competing with tree remnant overstory (e.g. *Nothofagus betuloides* can survive for long periods of time below the canopy) (Gutiérrez, 1994). However, *N. pumilio* regeneration only can survive few years in the seedling bank (<10 years and <10 cm height) (Cuevas, 2000; Martínez Pastur et al., 2011b), therefore competition could not explain this long time generated variability. This study shows that most of the variability could be a synergic effect between both browsing and climate-related damages. And also that forest regeneration can be successful despite browsing and climate-related damages.

Guanaco is a natural component of *Nothofagus* forests, and forests have naturally recovered from browsing successfully for thousands of years. On the other hand, there is no evidence that the presence of guanaco in forests has increased after introduction of sheep (Iranzo et al., 2013). In other temperate forests, browsing does not impede regeneration, but leads to changes in forest composition due to differential consumption according preference for some tree species (Edenius et al., 2002; Kribel et al., 2011). No evidence was found in our study that indicates guanaco is a limitation for the establishment and survival of forest regeneration in harvested stands or those damaged by windthrow. Some authors suggest that guanaco does not eliminate regeneration, but browsing affects shape and growth rate of plants, with important management consequences (Pulido et al., 2000; Cavieres and Fajardo, 2005). In the present work, we measured the impact of guanaco on regeneration height growth, but loss in quality over time still remains uncertain. Furthermore, we quantify the real benefits of mitigation actions (e.g. fencing and hunting), such as reduction of regeneration establishment time during shelterwood cuttings (30%–50% in time). However, incremental costs must be analysed in the framework of management planning of each forestry company. Conservation of ecosystems at landscape level depends on reconciling interests of livestock husbandry, guanaco conservation and timber industry (Moraga et al., 2015). For this, co-management of guanaco populations and forests requires good monitoring programmes for both components, as well as accurate ecological knowledge about the relations between guanacos and forage availability at different spatial levels, as proposed for moose in boreal managed forests (Edenius et al., 2002).

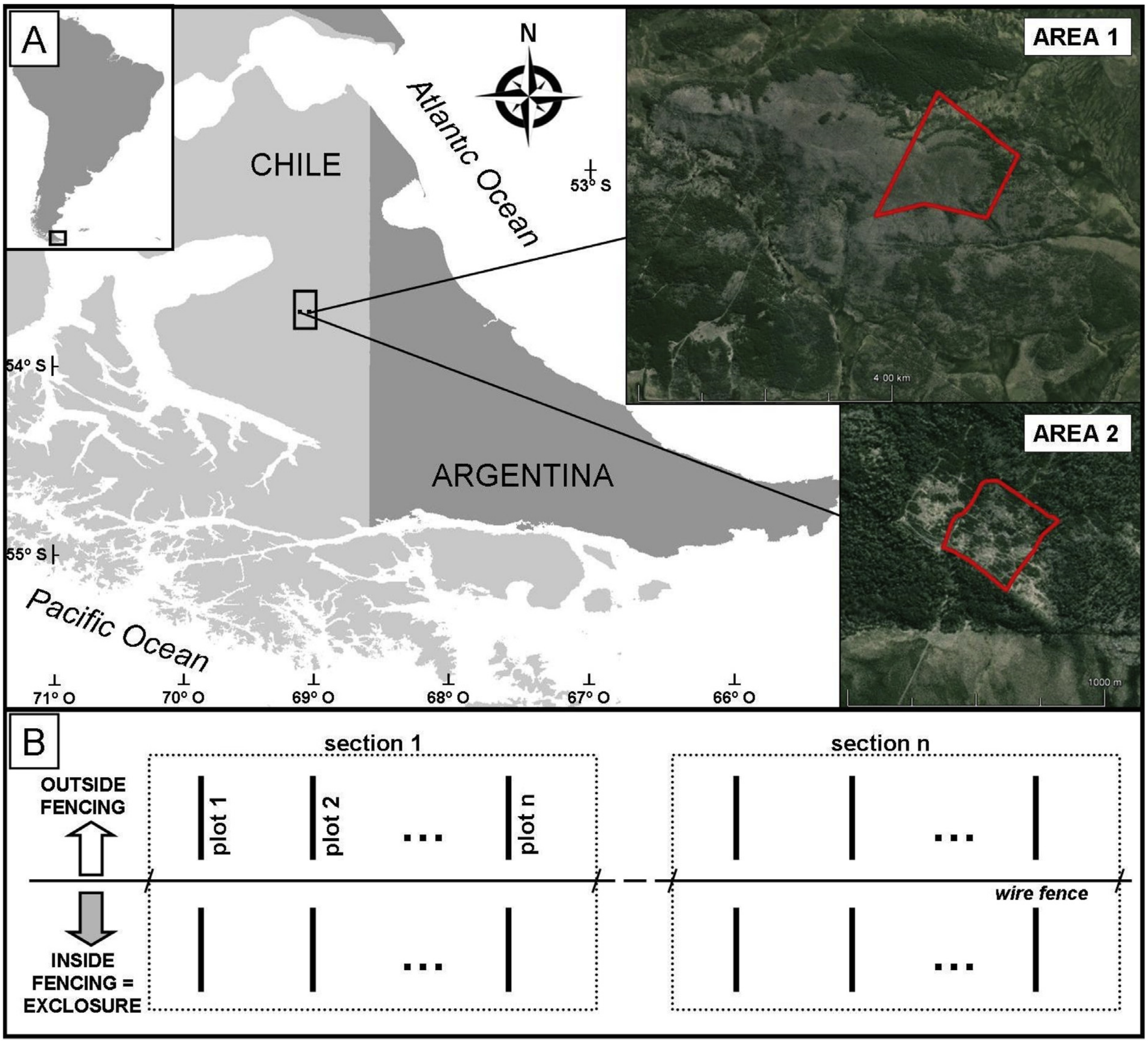
5. Conclusions

Harvested lenga forests with or without protective fences abundantly regenerate, including areas affected by windthrow, in presence of wild guanaco populations. Our study revealed that a reduction of guanaco density through hunting and fencing in harvested forests favoured height growth rate and decreased quality loss in regeneration. Beside this, in a comparison study we used two exclosures with different regeneration development (at the initial stage with <1.3 m high, and at the advanced stage with >1.3 m high) that demonstrated guanaco damages, which were different inside and outside exclosures in early stages, disappeared with time. Our study also demonstrated that climatic-related damages can produce synergies with browsing in quality loss of regeneration. This highlights the importance of considering this factor in future studies when analysing browsing effects. Finally, our study indicates that for best results, control of guanaco in recently harvested areas by fencing should be applied in combination with a reduction of guanaco density through continuous hunting. However additional long-term studies are necessary to quantify other benefits of these mitigation actions on time, due to, some of these benefits detected in early regeneration stages may vanish in later years.

Acknowledgements

This paper is in memory to Mauricio Rosenfeld, who promoted the study of forest management in Tierra del Fuego forests during all his professional life, and led us to conduct this research. We also want to thank Rodolfo Tirado and Luis Torres Garfia for their invaluable support, and for giving us crucial information on their management activities during data collection at FORESTAL RUSSFIN sawmill.

Annex



Annex 1. Sampling design: (A) Map of the research site with location of sampling areas (AREA 1 and AREA 2); wire fences are marked with red lines; and (B) plot layout with details of sections and plots inside and outside exclosure.

Annex 2
Multiple ANOVA for ground cover (average ± standard deviation) in AREA 1 considering fence section (1–4) and exclosure (inside and outside) as main factors, analysing woody debris by size in big (> 30 cm diameter), medium (5–30 cm) and fine (< 5 cm), or without debris (%).

Main factors		BIG (%)	MEDIUM (%)	FINE (%)	WITHOUT (%)
Section	1	19.9 ± 14.4	8.4 ± 5.6	5.2 ± 4.8	66.5 ± 16.6
	2	17.8 ± 11.0	9.7 ± 7.0	4.5 ± 2.9	68.1 ± 12.4
	3	19.5 ± 10.0	9.4 ± 6.4	4.2 ± 1.7	67.0 ± 12.2
	4	12.6 ± 7.5	10.0 ± 8.5	7.0 ± 3.9	70.5 ± 10.5
	$F_{3,72}(p)$	*1.82(0.150)*	*0.20(0.898)*	*2.63(0.056)*	*0.37(0.774)*
Exclosure	inside	16.2 ± 11.3	9.3 ± 7.3	4.6 ± 3.2	69.9 ± 12.3
	outside	18.7 ± 11.1	9.5 ± 6.5	5.8 ± 3.9	66.0 ± 13.4
	$F_{1,72}(p)$	*0.99(0.322)*	*0.02(0.898)*	*2.27(0.136)*	*1.76(0.188)*
Interaction	$F_{3,72}(p)$	*0.09(0.965)*	*1.15(0.336)*	*0.92(0.435)*	*0.94(0.428)*

$F_{s,r}(p)$ = Fisher test and significance between brackets, with "s" and "r" as degrees of freedom. Different letters indicate significant differences at p < 0.05 using Tukey test.

Annex 3

Multiple ANOVA for ground cover (average ± standard deviation) in AREA 2 considering fence section (1–6) and exclosure (inside and outside) as main factors, analysing woody debris by size in big (> 30 cm diameter), medium (5–30 cm) and fine (< 5 cm), or without debris (%)

Main factors		BIG	MEDIUM	FINE	WITHOUT
Section	1	16.7 ± 14.3	7.7 ± 8.1	2.7 ± 1.7	73.0 ± 14.3
	2	14.8 ± 14.2	10.2 ± 3.7	2.2 ± 2.3	72.8 ± 13.3
	3	13.1 ± 12.8	6.8 ± 3.5	1.4 ± 1.4	78.7 ± 15.4
	4	16.6 ± 16.2	6.8 ± 3.1	1.6 ± 1.6	75.0 ± 14.4
	5	10.5 ± 6.5	7.7 ± 5.5	3.3 ± 3.1	78.5 ± 10.6
	6	15.5 ± 8.2	10.3 ± 5.4	5.2 ± 6.0	69.0 ± 9.4
	$F_{5,28}(p)$	*0.22(0.949)*	*0.58(0.712)*	*1.29(0.295)*	*0.48(0.789)*
	inside	14.8 ± 12.2	7.9 ± 5.8	3.1 ± 3.7	74.2 ± 13.7
	outside	14.1 ± 12.4	8.5 ± 4.3	2.4 ± 2.4	75.0 ± 12.5
	$F_{1,28}(p)$	*0.04(0.851)*	*0.14(0.714)*	*0.46(0.502)*	*0.04(0.852)*
Interaction	$F_{5,28}(p)$	*0.71(0.620)*	*0.48(0.786)*	*0.79(0.564)*	*0.78(0.569)*

$F_{s,r}(p)$ = Fisher test and significance between brackets, with "s" and "r" as degrees of freedom. Different letters indicate significant differences at p < 0.05 using Tukey test.

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