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Landscape Variables Influence over Active Restoration Strategies of *Nothofagus* Forests Degraded by Invasive *Castor canadensis* in Tierra del Fuego

Guillermo J. Martínez Pastur [1,*], **Juan M. Cellini** [2], **María V. Lencinas** [1], **Yamina M. Rosas** [1], **Jonathan J. Henn** [3] and **Pablo L. Peri** [4]

1 Centro Austral de Investigaciones Científicas (CADIC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Houssay 200 (9400) Ushuaia, Tierra del Fuego, Argentina; mvlencinas@gmail.com (M.V.L.); yamicarosas@gmail.com (Y.M.R.)
2 Facultad de Ciencias Agrarias y Forestales, Universidad Nacional de la Plata (UNLP), Calle 60 y 118 (1900) La Plata, Buenos Aires, Argentina; cellini@gmail.com
3 Department of Biological and Environmental Sciences, University of Gothenburg, P.O. Box 461, 405 30 Gothenburg, Sweden; henn.jonathan@gmail.com
4 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; peri.pablo@inta.gob.ar
* Correspondence: gpastur@conicet.gov.ar

Abstract: North American beavers (*Castor canadensis*) are responsible for the major changes in the Tierra del Fuego Archipelago, altering riparian forests for the long-term. Passive restoration of the areas affected was ineffective in the medium-term (up to 20 years), being necessary active strategies. Plantations in abandoned ponds were made with *Nothofagus pumilio* and *N. antarctica* tree species across Tierra del Fuego island (Argentina). In the first experiment, we analysed the influence of biotic and abiotic factors in three micro-habitats in the impacted areas: front and tail of ponds, and cut not-flooded forest areas. Five-years-old *N. pumilio* seedlings had 39% survival in front, 21% in tails, and 46% in cut areas at year-3 of the restoration experiments, being negatively influenced by plant cover and soil moisture. Lower growth was recorded during year-1 (0.7–0.9 cm yr^{-1}), but increased on time (1.9 cm yr^{-1} front, 1.6 cm yr^{-1} tail, 4.3 cm yr^{-1} cut areas). A second experiment explores the alternative to substitute the tree species to face the harder conditions of the impact and climate change. For this, we conducted a new plantation at four locations across the main bioclimatic zones, where 10–40 cm *N. antarctica* plants attained 17% survival in meadows (front and tail) and 30% in cut areas, being higher with larger than smaller plants (25% vs. 18%), and where they are mainly influenced by rainfall (4% in sites <400 mm yr^{-1} and 41% in >400 mm yr^{-1}). The main damage was detected in the above-ground biomass due to dryness, but root survival allowed the emergence of new shoots in the following growing season. It is necessary to monitor different *Nothofagus* species across natural environments in the landscape to determine the feasibility and effectiveness of different strategies in restoration plans, considering the selection of climate-resilient tree species.

Keywords: Patagonia; plantation; invasive species; species substitution; climate change

1. Introduction

Invasive species are the most important drivers of change in natural environments [1,2], modifying ecosystem services, biodiversity and ecological functions [3,4]. Many of these alterations can have permanent legacies, and require active interventions to restore the natural values and services [5–7]. One of the most dramatic alterations to southern forest ecosystems of the last century is related to the invasion of North American beavers (*Castor canadensis*) in the Tierra del Fuego Archipelago [8], which extensively alter riparian forests and have become the most relevant issue of conservation concern in southern Patagonia to maintain the provision

of ecosystem services [9]. As ecosystem engineers, beavers generate extensive impacts on the environmental conditions of streams and riparian zones [10], including: (i) flooding areas that removed tree canopy cover and accumulates sediments that leads to changes in soil properties, and (ii) areas where trees are harvested (30–60 m from beaver ponds) [4,11–14]. The first impact type altered the natural dynamics, leading to long-term changes from forest to grassland meadows, where the front of the beaver ponds (the area near the dam) is wetter and contains more organic sediment compared to the tail (the area where the stream enters to the ponds) [4,15]. The second impact type was similar to those observed in natural dynamics (e.g., local windthrow) or commercial harvesting, allowing an increase in the natural regeneration establishment and growth, recovering the impacted areas on time [16–18].

Nothofagus species are the dominant trees in Tierra del Fuego, and are not adapted to beaver-induced changes [6]. This vulnerability is related to changes in the microclimate, invasive understory plants, suppression of native species, loss of riparian forest characteristics, alteration of natural ecological cycles, nutrient loss, and changes in soil properties [4,8,14,19–22]. While the natural regeneration process is not affected by beaver foraging in the adjacent unflooded areas, the flooded portions lose their seedling bank and lack recruitment, even after more than 20 years since abandonment [8]. Beaver meadows appear to be an alternative or long-term stable state other than closed forests, and therefore active intervention is likely required to achieve forest regeneration over the short- and medium-term [9,14]. However, the main thresholds for natural *Nothofagus* regeneration are not clear, so it is necessary to determine these thresholds before active restoration strategies are designed. Some authors suggest that the changes in the soil properties are the main negative issue, however other authors suggest that the main reason is competition with the herbaceous community beaver meadows [4]. However, other reasons can be related to seed availability due to the lack of remnant overstory [23], or changes in the water table dynamics affecting the physiological performance of some tree species (e.g., *N. pumilio*) [17,24]. Because of this, it was suggested that other species that can tolerate beaver meadow conditions can be better candidates for active restoration in the beaver-impacted areas (e.g., *N. antarctica*) [25]. Finally, the climate also influences the landscape, where different strategies can be followed according to the climatic context, e.g., northern ecotone forests presenting higher summer temperatures and lower rainfall throughout the year compared to southern mountain forests [26,27].

Argentina and Chile signed an agreement to eradicate invasive species due to the low resilience of Patagonian forests to the impacts generated by beavers [4,6]. In fact, passive restoration of the areas affected was ineffective in the medium-term (up to 20 years), making active strategies necessary for forest restoration [8]. In this framework, the objective of this work was to determine the influence of the landscape over active restoration strategies of *Nothofagus* forests degraded by invasive beavers in Tierra del Fuego. We intend to answer the following questions to develop better restoration strategies: (i) do the stand characteristics and natural dynamics (abiotic, soil, forest structure, understory, litter, seeding, regeneration) change within beaver meadows and unimpacted forests across the landscape?, (ii) can *N. pumilio* seedlings survive in the short-term (three growing seasons) to these modified environments?, and (iii) do early succession forest species (e.g., *N. antarctica*) improve the active restoration across the landscape? Through these questions, first we want to determine the impact produced by the beavers that impede the passive restoration in the long-term (up to 20 years according to [8]), and specifically analyse the feasibility of survival of *N. pumilio* seedlings based on a manipulative experiment.

With these results, we expect to determine the main bottlenecks of the passive restoration, and the potential success of the active restoration using the climax tree species (*N. pumilio*). Secondarily, we want to know if the use of a climate-resilient tree species (*N. antarctica*) can improve the active restoration across the temperature and rainfall gradients in the landscape. We hypothesized that there are beaver-caused changes in the abiotic and biotic environment of abandoned beaver meadows, which are responsible for the observed lack of *N. pumilio* regeneration [4], and generate inadequate conditions for natural

regeneration recruitment and survival, generating a reduction in the eco-physiological performance of the seedlings (e.g., [17,24,28]). Beside this, we expect that an early succession tree species, such as *N. antarctica*, can present a better performance in these modified environments due to its eco-physiological characteristics (e.g., [25]) allowing to a quick recovery of the impacted areas (from meadows to forest environments), and their ecological functions and ecosystem services. These early succession forests can recover some micro-environmental conditions that allowed the recruitment, survival and growth of the *N. pumilio* regeneration (e.g., [18]) and the recovery of other species of the original ecosystem with local extinction (e.g., [29]).

2. Materials and Methods

2.1. Study Area

Four forested landscapes were selected across Tierra del Fuego island (Argentina) dominated by old-growth *N. pumilio* stands (>200 years old). This is the dominant tree species in the landscape. It is a native broadleaf deciduous tree, medium shade-intolerant that could live more than 400 years, whose foliation is from October to April. Flowering is on November, its fruits rapidly develop to mature in late March, and immediately dispersing seeds by wind. These forests naturally regenerate from seedlings, which could survive many years in the understory until microclimatic conditions facilitate their height growth. The understory plant diversity is poor and has low cover (<40%), being inhabited by few shrubs (<50 cm height), and several herbs and grasses [4,6,8,23,28,29].

These areas were selected across a climate gradient from cool and wet to warm and dry conditions (Figure 1A,B): (i) Tierra del Fuego National Park (NP) (54°51′ S, 68°34′ W) (–temperature, ++rainfall) with a mean annual temperature (MAT) of 3.0 °C and an average rainfall (AR) of 50.9 mm month^{-1}, (ii) Irigoyen river (IRI) (54°37′ S, 66°42′ W) (-temperature, +rainfall) with MAT of 4.2 °C and AR of 44.3 mm month^{-1}, (iii) Valdéz river (VAL) (54°38′ S, 67°22′ W) (+temperature, -rainfall) with MAT of 4.3 °C and AR of 40.5 mm month^{-1}, and (iv) Los Cerros ranch (LC) (54°22′ S, 67°51′ W) (++temperature, –rainfall) with MAT of 4.7 °C and AR of 37.6 mm month^{-1} [26]. Plots were established in abandoned beaver meadows, where beavers occupied the areas since the 1960s and 1970s, affecting most of the riversides [6].

At each study area, we studied four zones (Figure 1C,D) based on previous studies [4,8]. Three located in the beaver meadows: (i) front (FRO, area just upstream of the old dam), (ii) tail (TAI, area where stream enters beaver meadow), and (iii) cut (CUT, area harvested, but not flooded, by beavers); and one located in one adjacent unimpacted old-growth forests (OGF) acting as a control forests (OGF). The design is justified in the changes of sediment dynamics and the nutrient cycling due to flooding [30], and the influence of canopy cover (Figure 2) over the natural regeneration dynamics and the beaver foraging effects [8,18,23]. Active beaver dams have not existed in the study areas for at least five years. Forest degradation is evident due to the lack of living trees in the abandonment meadows and the severely limited established natural tree regeneration (Figure 1D).
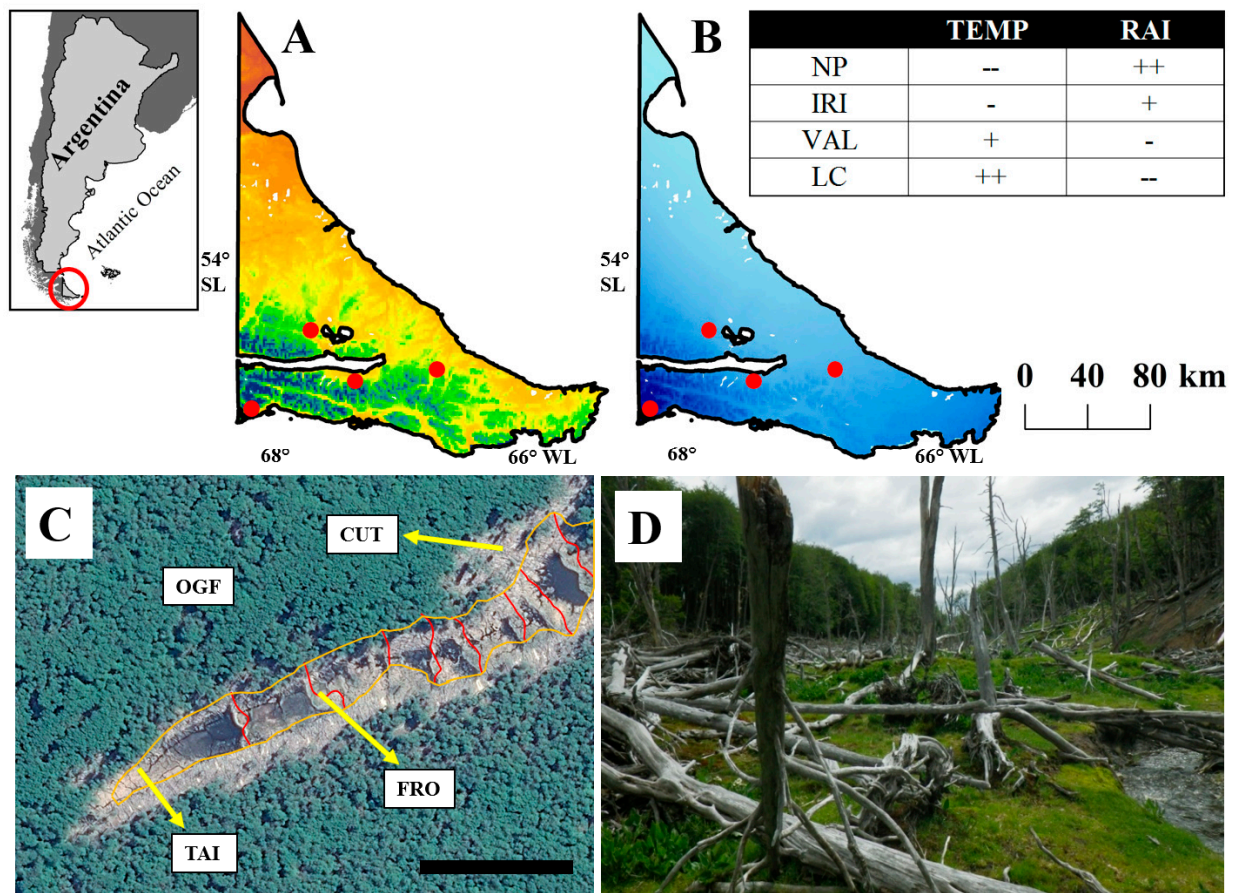
Figure 1. Location of the study area at the southern portion of Argentina (red circle) and locations (red dots) where NP = Tierra del Fuego National Park, VAL = Río Valdez, IRI = Río Irigoyen, LC = Los Cerros, showing (**A**) mean annual temperature (0.1 to 6.9 °C) (red is high and blue is low), (**B**) mean annual rainfall (253 to 721 mm yr^{-1}) (dark colour means higher values), (**C**) forest treatments (FRO = area just upstream of the old dam, TAI = area where stream enters beaver meadow, CUT = area harvested, but not flooded, by beavers, OGF = adjacent unimpacted old-growth forest), where red lines identify old and new dams, orange line identifies boundary within harvested and flooded areas, and black line representing 100 m, and (**D**) general view of one abandoned meadow where the plantations were conducted.

Figure 2. Examples of hemispherical photos to illustrate the overstory cover in the forest treatments: **Left** = adjacent unimpacted old-growth forest (OGF), **Middle** = area harvested, but not flooded, by beavers (CUT), and **Right** = beaver meadow (FRO = area just upstream of the old dam, and TAI = area where stream enters beaver meadow).

2.2. Characterization of the Study Sites

Forest structure was measured with the Bitterlich [31] point sampling method (K between 1 and 7), using a Criterion RD1000 and TruPulse 200 laser rangefinder (Laser Technology, Centennial, CO, USA) (4 forests × 4 treatments × 5 replicas = 80 plots). At each plot, diameter at breast height (DBH, cm) of all live trees >5 cm was measured to calculate basal area (BA, m^2 ha^{-1}), and the height of two dominant trees (DH, m) as a proxy of productivity of the site. Hemispherical photos were taken from 1 m above the ground during January with an 8-mm fish-eye lens (Sigma, Kawasaki-shi, Japan) mounted on a 35-mm digital camera (Nikon, Tokyo, Japan) with a tripod and level which were oriented to the magnetic north. The program Gap Light Analyzer v2.0 was used to calculate crown overstory cover (CC, %), relative leaf area index (RLAI) and the incidence of total radiation (TR, %). For details of inputs and models, see Martinez Pastur et al. [18]. In the same plots, natural regeneration density (NRD, $n\ m^{-2}$) and plants damage by browsing (BRO, %) were measured in strip plots (5 × 0.2 m). Additionally, four soil samples (0–10 cm depth) were collected using a field borer with known volume (230.9 cm^3) after previously removing the litter layer. Samples were weighted before and after air-drying in laboratory conditions (24 °C) until constant weight. Soil bulk density (SBD, $g\ cm^{-3}$) and soil moisture (SM, %) were obtained from the average of four samples. After that, coarse root debris >2 mm and soil aggregations (e.g., small, large and sand-sized stones) had been removed by sieving, and then we pooled individual soil samples into one combined sample per plot. Samples were finely ground to below 2 mm using a tungsten-carbide mill, washed with HCl (50%) and then total organic carbon (C, %) was determined by an automatic analyser (LECO CR12, St. Joseph, MI, USA).

At the same plots, one seed trap (40 × 40 cm) was placed during mid-summer (January) and collected after litter-fall occurred in late autumn (May). Trap contents were manually separated and analysed in the laboratory, quantifying: total seeds (S, thousand ha^{-1} yr^{-1}), seeds foraged by insects (SI, thousand ha^{-1} yr^{-1}), seeds foraged by birds (SB, thousand ha^{-1} yr^{-1}), seed weight (SW, kg ha^{-1} yr^{-1}), weight of the leaf litter (LW, kg ha^{-1} yr^{-1}), and small branches (<1 cm) of the litter (BW, kg ha^{-1} yr^{-1}). Foraging by birds or insects was determined by scars and damage on the collected seeds (see [32]).

A complementary, more specific sampling was conducted only at the Irigoyen river (IRI) study area (see more details in [4]) (3 meadows × 4 treatment areas × 4 replicate plots = 48 samples). Using the same soil sampling technique, we additionally measured total nitrogen (N, %) by a semi-micro Kjeldahl method, and extractable phosphorous (P, ppm) according to the method of Bray and Kurtz [33]. Cation exchange capacity (CEC, meq 100 gr) was measured with an ICP-AES (Optima 3000, Perkin-Elmer, Barcelona, Spain) in an unbuffered solution of 1 M NH_4Cl for 1 h on a shaker using a soil extract ratio of 1:10. Understory plants (MONO = monocots, DICO = dicots, NV = non-vascular plants as ferns, mosses and lichens, and TREE = overstory trees) and bare soil cover (BS, %) were measured by 50 intersection points along the regeneration plot transect. Finally, mean distances to the forest edge (DIST, m) were also measured with the TruPulse 200 laser rangefinder.

2.3. Transplantation and Measurement Design

The first experiment was conducted at the Irigoyen river (IRI) within beaver meadow areas (FRO, TAI, CUT), where 36 regeneration plots (3 meadows × 3 treatment areas × 4 replicate plots) were established by clearing all existing vegetation in 0.25 m^2 areas, and planting 2–4 year-old *N. pumilio* seedlings in a 10 × 10 cm^2 grid (*n* = 100). Seedlings were approximately 5 cm tall and were collected from adjacent forests by carefully pulling the plants out of litter to prevent breaking and losing fine roots. Transplanting occurred in late October, before the start of the growing season. Survival (SUR, %), seedling height (H, cm), and the number of leaves (LEA) were measured monthly during the growing season (December to April) from 2012 to 2015. At the end of the first year since the plantation, the biometry of the seedlings was studied, and two plants per plot were removed, and the seedling height, root length (R, cm), foliar area (FA, cm^2), leaves weight (LW, gr), steam weight (SW, gr), and roots weight (RW, gr) were measured at the laboratory.

The second experiment was conducted at the four study sites, also within beaver meadow areas (FRO, TAI, CUT), analysing the effect of the landscape and regional climate. *N. antarctica* seedlings were collected from one peatland (54°37′ S, 67°46′ W) and bare root plants were transplanted during early autumn (April) at the end of the growing season. The plants were extracted from a peatland because they are adapted to water-saturated soils (similar to meadows conditions), and because the extraction was facilitated by the soft peat substrate, preventing breaking and loss of fine roots. Plants were classified in two types (BIG = big plants with 15–30 cm height, SMA = small plants with <15 cm height). The final design including 96 transplanting plots of 10 × 10 m with 25 plants each one (4 areas × 3 treatments × 2 types × 4 replicates) without clearing the existing vegetation. Survival, seedling height, and growth defined as the changes in length of the extended dominant branch growing during the studied growing season (GRO, cm month^{-1}) were measured monthly during one growing season (December to April).

A summary of the variables employed in the whole study was presented in the Appendix A.

2.4. Statistical Analyses

Six groups of multiple ANOVAs were conducted to characterize the study sites and the transplanting experiments, evaluating: (i) forest structure (DH, BA, CC, RLAI), environmental characteristics (TR, SM, SBD, C) and natural regeneration (NRD, BRO) considering forest treatments (FRO, TAI, CUT, OGF) and locations (NP, VAL, IRI, LC) as main factors; (ii) soil properties (N, C/N, P, CEC), plant community cover (DICO, MONO, INF, BS) and mean distance to forest edge (DIST) considering forest treatments (FRO, TAI, CUT, OGF) and meadows (1, 2, 3) as main factors; (iii) natural seed production (S, SI, SB, SW) and litter (LW, BW) considering forest treatments (FRO, TAI, CUT, OGF) and locations (NP, VAL, IRI, LC) as main factors; (iv) plantation of *N. pumilio* (SUR, H, LEA) considering forest treatments (FRO, TAI, CUT, OGF), meadows (1, 2, 3) and time (days or years) as main factors; (v) plantation of *N. pumilio* after one-year (H, R, FA, LW, SW, RW, S/R) considering forest treatments (FRO, TAI, CUT) and meadows (1, 2, 3) as main factors; and (vi) plantation of *N. antarctica* after one-year (SUR, H, GRO) considering forest treatments (FRO, TAI, CUT), locations (NP, VAL, IRI, LC), plant type (BIG, SMA) and time (month) as main factors. ANOVAs were conducted using Fisher test and Tukey test at p <0.05 to separate means. To avoid pseudo-replication, the measurements from each plot at each area were averaged before analyses.

3. Results

3.1. The Impact of Beavers and the Variations through the Landscape

Dominant height, as a proxy of site quality, did not change in areas impacted by beavers compared to OGF. However, it was different across the four study sites (LC > IRI > VAL > NP) (Table 1), following the rainfall and temperature gradients (Figure 1). Remnant BA was lowest in the old beaver dams (FRO and TAI) where flooding also impacted tree survival, compared to those areas just foraged (CUT), representing 1.3%, 4.9% and 23.3% BA compared to control sites (OGF). This decrease in BA also decreased CC and RLAI, increasing TR at floor level (Figure 2). The magnitude of the beaver impact of the studied variables was not homogeneous at the landscape level (NP > LC > VAL > IRI) and not follow evident environmental gradients. The reduction in the overstory and the flooding significantly modified soil moisture (FRO-TAI > CUT-OGF) and soil characteristics, decreasing SBD and increasing C content. The magnitude of these changes was not homogeneous through the landscape, where soil characteristics (SM, SBD, C) were associated with the climate gradients (SM and C increasing with rainfall and decreasing with temperature, and SBD follow a contrary pattern). Other soil characteristics were only studied at one site (IRI), where N and CEC increased and P decreased in the impacted areas (FRO, TAI, CUT) compared to OGF (Table 2). However, N and CEC changed across different meadows while P did not change, probably due to their location (e.g., closeness

of meadow 3 to peatlands, however meadow 2 presented the lower values in most of the studied variables). Finally, the C/N ratio did not show significant differences.

Changes in forest structure positively affected natural regeneration dynamics, however the changes in the soil characteristics generated positive and negative relationships or promoted trade-offs with other species groups (e.g., understory plants or natural populations of *Lama guanicoe*). The harvesting due to beaver foraging increased the regeneration density and browsing damages compared to OGF, however, flooding (FRO and TAI) significantly decreased the number of plants and browsing effects (Table 1). Tree regeneration varied greatly across the landscape (IRI > VAL > LC > NP) following unexpected patterns, while browsing was directly related to *L. guanicoe* wild populations living at each area. Regeneration decreased in the meadows due to the increase in monocots in the understory (Table 2), and also by the increase in mosses and liverworts in FRO areas (Figure 1D). Besides, the decrease in bare soil and the increase in the distance to the forest edge can be an impediment for seed arrival and seedling establishment. Most of these soil cover characteristics were maintained through the IRI study area, however inferior plants are not homogeneous at the different meadows.

We only surveyed one year of seed and litter production to support the described regeneration behaviour (Table 3). Seeds arriving at the different areas were directly related to the remnant overstory (OGF > CUT > FRO-TAI), and natural foraging (insects and birds) mainly occurred in non-flooded areas (CUT and OGF) but without significant differences. The same pattern was observed for SW, indicating that seeds that arrived at the flooded areas (FRO and TAI) were 3 times smaller than at CUT and OGF areas. This is closely related to the distance to the edges (Table 2). Litter and small branches were directly related to the remnant overstory and the distance to the forest edges (Table 1), and significantly decreasing the input of tree biomass to the floor across the year. When the differences were compared at the landscape level (Table 3), seed production was greater at IRI where the most NRD was found (Table 1). Besides, bird foraging was higher where seed production was high and attractive for birds to forage there (VAL-IRI compared to NP-LC). Considering the seed size, the NP study area presented the smaller seeds, while the other variables followed the described patterns.

Table 1. Multiple ANOVAs of forest structure, environmental characteristics and natural regeneration among forest treatments (FRO = area just upstream of the old dam, TAI = area where stream enters beaver meadow, CUT = area harvested, but not flooded, by beavers, OGF = adjacent unimpacted old-growth forest) and locations (NP = Tierra del Fuego National Park, VAL = Río Valdez, IRI = Río Irigoyen, LC = Los Cerros) analysing: DH = dominant overstory height (m), BA = basal area (m^2 ha^{-1}), CC = crown overstory cover (%), RLAI = relative leaf area index, TR = incidence of total radiation (%), SM = soil moisture (%), SBD = soil bulk density (g cm^{-3}), C = carbon (%), NRD = natural regeneration density (n m^{-2}), and BRO = damage plants by browsing (%).

Treatment	Level	DH	BA	CC	RLAI	TR	SM	SBD	C	NRD	BRO
A: Forest	FRO	19.30	0.81a	36.38a	0.13a	82.0c	72.4c	0.27a	23.7bc	1.25a	0.00a
	TAI	17.93	2.87a	34.41a	0.12a	83.6c	73.5c	0.23a	25.2c	0.62a	0.00a
	CUT	19.16	13.56b	48.56b	0.54b	65.5b	34.7a	0.57c	9.9a	94.37b	16.25b
	OGF	17.70	58.25c	81.84c	1.99c	22.8a	43.6b	0.44b	17.3b	55.00b	3.12a
	F	2.61	318.38	380.68	166.96	420.84	86.06	24.42	16.47	14.96	21.18
	(*p*)	(0.061)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)
B: Location	NP	12.39a	13.25a	49.70b	0.50a	68.0b	71.7c	0.24a	22.4bc	6.87a	0.00a
	VAL	17.84b	20.75bc	44.58a	0.66a	65.5b	57.1b	0.33a	23.8c	20.62a	3.75a
	IRI	21.14c	24.56c	63.83c	0.96b	52.1a	49.8ab	0.45b	16.5ab	96.87b	10.62b
	LC	22.71c	16.93ab	43.09a	0.66a	68.5b	45.7a	0.49b	13.4a	26.87a	5.00ab
	F	80.51	10.50	70.71	7.84	31.39	28.63	16.33	8.15	11.7	6.84
	(*p*)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)
AxB	F	1.45	2.51	5.08	2.09	2.46	4.77	2.83	3.65	6.09	3.47
	(*p*)	(0.194)	(0.019)	(<0.001)	(0.049)	(0.022)	(<0.001)	(0.009)	(0.015)	(<0.001)	(0.002)

F = F test, *p* = probability. Different letters showed significant differences using Tukey test ($p \leq 0.05$).

Table 2. Multiple ANOVAs of soil properties, floor cover and mean distance to forest edge in Río Irigoyen among treatments (FRO = area just upstream of the old dam, TAI = area where stream enters beaver meadow, CUT = area harvested, but not flooded, by beavers, OGF = adjacent unimpacted old-growth forest) and meadows (1 to 3), analysing: N = nitrogen (%), C/N = ratio carbon/nitrogen, P = phosphorous (ppm), CEC = cation exchange capacity (meq 100 gr), MONO = monocot plants (%), DICO = dicot plants (%), NV = non-vascular plants (%), TREE = overstory trees (%), BS = bare soil (%), and DIST = mean distance to the forest edge (m).

	Level	N	C/N	P	CEC	MONO	DICO	NV	TREE	BS	DIST
A: Forest	FRO	1.46b	12.05	10.31a	87.52c	31.9b	42.9	21.7b	0.0a	3.5a	19.4b
	TAI	1.28ab	11.88	10.56a	68.83ab	39.8b	55.4	3.5a	1.2ab	0.0a	20.6b
	CUT	1.44ab	11.90	15.75ab	71.46bc	2.0a	54.1	4.6a	7.2b	30.1b	4.7a
	OGF	1.09a	12.23	25.04b	52.62a	–	–	–	–	–	–
	F	3.18	0.50	3.85	9.63	43.50	1.39	11.42	4.06	11.83	98.56
	(*p*)	(0.035)	(0.682)	(0.017)	(<0.001)	(<0.001)	(0.266)	(<0.001)	(0.029)	(<0.001)	(<0.001)
B: Meadow	1	1.26b	11.80	14.28	73.82b	19.9	40.0	17.2b	3.4	19.41	16.15
	2	0.93a	11.88	13.84	43.70a	24.7	60.3	0.4a	1.7	11.25	15.44
	3	1.76c	12.36	18.13	92.80c	29.1	52.1	12.1b	3.3	2.92	13.12
	F	25.02	2.36	0.60	38.51	2.34	3.09	8.18	0.27	2.97	3.15
	(*p*)	(<0.001)	(0.108)	(0.552)	(<0.001)	(0.115)	(0.062)	(0.002)	(0.765)	(0.068)	(0.059)
AxB	F	5.18	0.46	3.10	7.97	2.32	5.13	4.39	0.43	1.93	11.61
	(*p*)	(0.001)	(0.832)	(0.015)	(<0.001)	(0.083)	(0.003)	(0.007)	(0.786)	(0.134)	(<0.001)

F = F test, *p* = probability. Different letters showed significant differences using Tukey test ($p \leq 0.05$).

Table 3. Multiple ANOVAs of natural seed production and litter among forest treatments (FRO = area just upstream of the old dam, TAI = area where stream enters beaver meadow, CUT = area harvested, but not flooded, by beavers, OGF = adjacent unimpacted old-growth forest) and locations (NP = Tierra del Fuego National Park, VAL = Río Valdez, IRI = Río Irigoyen, LC = Los Cerros) analysing: S = total seeds (thousand ha^{-1} yr^{-1}), SI = seeds foraged by insects (thousand ha^{-1} yr^{-1}), SB = seeds foraged by birds (thousand ha^{-1} yr^{-1}), SW = seed weight (kg ha^{-1} yr^{-1}), LW = leaves weight of the litter (kg ha^{-1} yr^{-1}), and BW = small branches (<1 cm) of the litter (kg ha^{-1} yr^{-1}).

Treatment	Level	S	SI	SB	SW	LW	BW
A: Forest	FRO	31.3a	0.0	0.0	0.15a	84.7a	19.0ab
	TAI	18.8a	0.0	0.0	0.04a	92.9a	4.6a
	CUT	1241.3b	34.7	29.9	14.21a	862.0b	39.8bc
	OGF	3181.4c	21.7	32.8	33.57b	3222.0c	306.5c
	F	26.37	1.26	2.25	14.92	114.39	11.15
	(*p*)	(<0.001)	(0.293)	(0.086)	(<0.001)	(<0.001)	(<0.001)
B: Location	NP	824.6a	0.0	0.0a	1.47a	1056.5ab	102.7ab
	VAL	1077.4a	0.0	112.8b	13.22a	689.2a	117.8ab
	IRI	2201.9b	34.7	30.4ab	28.19b	1492.4b	220.4b
	LC	368.9a	21.7	0.0a	5.08a	1023.7a	55.7a
	F	8.53	1.30	3.39	8.94	7.43	3.14
	(*p*)	(<0.001)	(0.277)	(0.021)	(<0.001)	(<0.001)	(0.028)
AxB	F	3.01	1.28	2.17	3.32	5.86	1.81
	(*p*)	(0.003)	(0.257)	(0.029)	(0.001)	(<0.001)	(0.073)

F = F test, *p* = probability. Different letters showed significant differences using Tukey test ($p \leq 0.05$).

3.2. Manipulative Assay of Nothofagus Pumilio Regeneration Survival and Growth

Transplanted seedlings at IRI study site showed greater survival in CUT areas and near the dams (FRO) compared to tail parts of the meadows (TAI) (Table 4), however, there were differences among the studied meadows (meadow 2 showed lower performance) (Table 4). The survival rate decreased in time along the three years surveyed (Figure 3). Mortality occurred during the whole year, including the winter time, for all treatments but decreased in magnitude across the years (Table 4).

Height growth was higher in CUT areas compared to the treatment located in the meadows (FRO and TAI), and increased across the years (Table 4). The number of leaves per seedling did not vary among the treatments or studied meadows, and as expected, increased across the years. These growth differences were not significant at the end of the first season, when a destructive analysis was conducted (Table 5). We expect to find more differences in the root development (e.g., CUT > FRO-TAI), but they were non-significant.

Table 4. Multiple ANOVAs of seedlings plantation of *Nothofagus pumilio* in Río Irigoyen among forest treatments (FRO = area just upstream of the old dam, TAI = area where stream enters beaver meadow, CUT = area harvested, but not flooded, by beavers, OGF = adjacent unimpacted old-growth forest), meadows (1 to 3) and time measured by days (i) or years (ii), analysing: SUR = survival (%), H = seedling height (cm), and LEA = number of leaves.

(i)	Level	SUR	(ii)	Level	H	LEA
A: Forest	FRO	61.0b	A: Forest	FRO	12.1a	6.2
	TAI	41.9a		TAI	11.0a	6.7
	CUT	64.5b		CUT	22.4b	6.9
	F	84.57		F	19.06	0.50
	(*p*)	(<0.001)		(*p*)	(<0.001)	(0.611)
B: Meadow	1	66.7c	B: Meadow	1	16.6	7.9
	2	40.7a		2	14.2	5.4
	3	60.1b		3	14.7	6.5
	F	104.62		F	0.76	5.47
	(*p*)	(<0.001)		(*p*)	(0.469)	(0.005)
C: Time	0	100.0i	C: Time	2012	5.6a	3.0a
	30	87.2hi		2013	7.9a	3.4a
	60	80.4gh		2014	20.0b	5.6b
	90	73.7fgh		2015	27.1c	14.4c
	120	66.8efg		F	31.29	61.81
	150	62.6def		(*p*)	(<0.001)	(<0.001)
	395	55.4cde	AxBxC	F	0.76	0.64
	425	50.6bcd		(*p*)	(0.603)	(0.697)
	455	47.8bcd				
	485	46.1abc				
	515	45.7abc				
	760	40.4ab				
	791	37.5ab				
	819	36.2ab				
	850	31.9a				
	881	31.5a				
	F	45.99				
	(*p*)	(<0.001)				
AxBxC	F	0.29				
	(*p*)	(0.999)				

F = F test, *p* = probability. Different letters showed significant differences using Tukey test ($p \leq 0.05$).
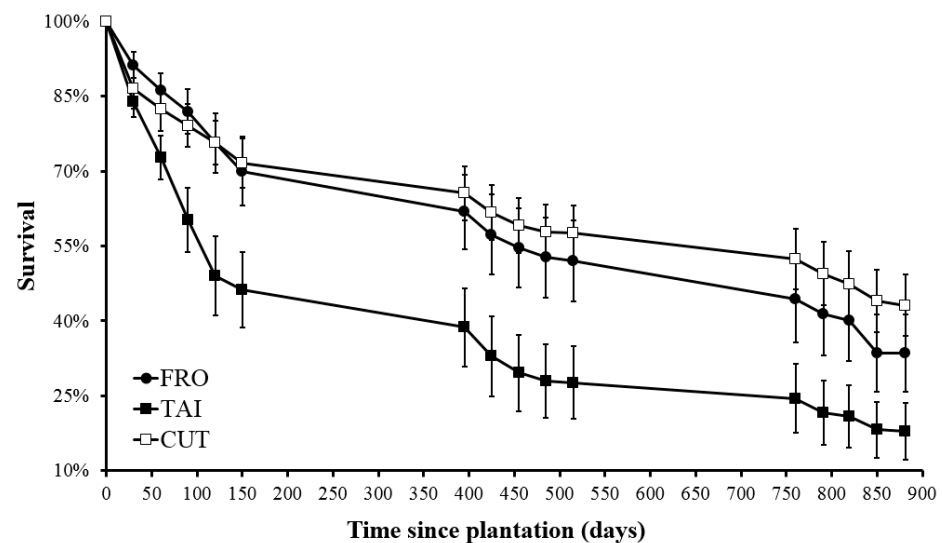
Figure 3. Survival of seedlings plantation of *Nothofagus pumilio* in Río Irigoyen among forest treatments (FRO = area just upstream of the old dam, TAI = area where stream enters beaver meadow, CUT = area harvested, but not flooded, by beavers) and time since plantation.

Table 5. Multiple ANOVAs of seedlings plantation of *Nothofagus pumilio* in Río Irigoyen after one-year among forest treatments (FRO = area just upstream of the old dam, TAI = area where stream enters beaver meadow, CUT = area harvested, but not flooded, by beavers, OGF = adjacent unimpacted old-growth forest) and meadows (1 to 3), analysing: H = seedling height (cm), R = root length (cm), FA = foliar area (cm^2), LW = leaves weight (gr), SW = steam weight (gr), RW = roots weight (gr), and S/R = steam/root weight ratio.

	Level	H	R	FA	LW	SW	RW	S/R
A: Forest	FRO	4.7	6.2	2.3	0.04	0.04	0.06	78.1
	TAI	4.3	5.1	2.4	0.04	0.04	0.05	82.5
	CUT	4.9	5.4	2.3	0.03	0.05	0.06	97.1
	F	1.06	1.17	0.03	0.53	0.97	0.60	0.68
	(*p*)	(0.359)	(0.326)	(0.968)	(0.597)	(0.390)	(0.556)	(0.517)
B: Meadow	1	4.5	5.4	2.2	0.04	0.04	0.05	77.9
	2	5.0	5.6	2.4	0.04	0.04	0.06	86.1
	3	4.4	5.7	2.5	0.04	0.05	0.06	93.9
	F	1.69	0.09	0.47	0.08	0.65	0.11	0.43
	(*p*)	(0.204)	(0.916)	(0.633)	(0.927)	(0.528)	(0.898)	(0.652)
AxB	F	2.12	0.81	3.88	5.28	2.14	1.08	0.55
	(*p*)	(0.105)	(0.528)	(0.013)	(0.003)	(0.103)	(0.385)	(0.703)

F = F test, *p* = probability. Different letters showed significant differences using Tukey test ($p \leq 0.05$).

3.3. Performance of Early Succession Nothofagus Antarctica Tree Species in Restoration Plantations

The survival rate after the first growing season was higher in CUT areas compared to the meadows (FRO and TAI), however, the growth was lower (FRO > TAI > CUT) (Table 6). Bigger transplanted plants presented a higher survival rate, and as was expected, they achieved greater height. These performances were not homogeneous across the landscape, being higher at the southern study site (NP with more rainfall and cooler temperatures) and lower at the northern study site (LC with less rainfall and warmer temperatures). However, growth was higher in VAL and IRI sites (0.70–0.89 compared to 0.53–0.13 cm month^{-1}). The survival rate decreased through time along the studied season (Figure 4). Mortality occurred throughout the year for all treatments, as well as H and GRO (Table 6). However, some treatments and locations were heavily impacted by the winter, and few

plants survived (e.g., small plants at LC study site). The magnitude of this impact follows the rainfall and temperature gradient across the landscape, decreasing when temperature decreased and when rainfall increased.
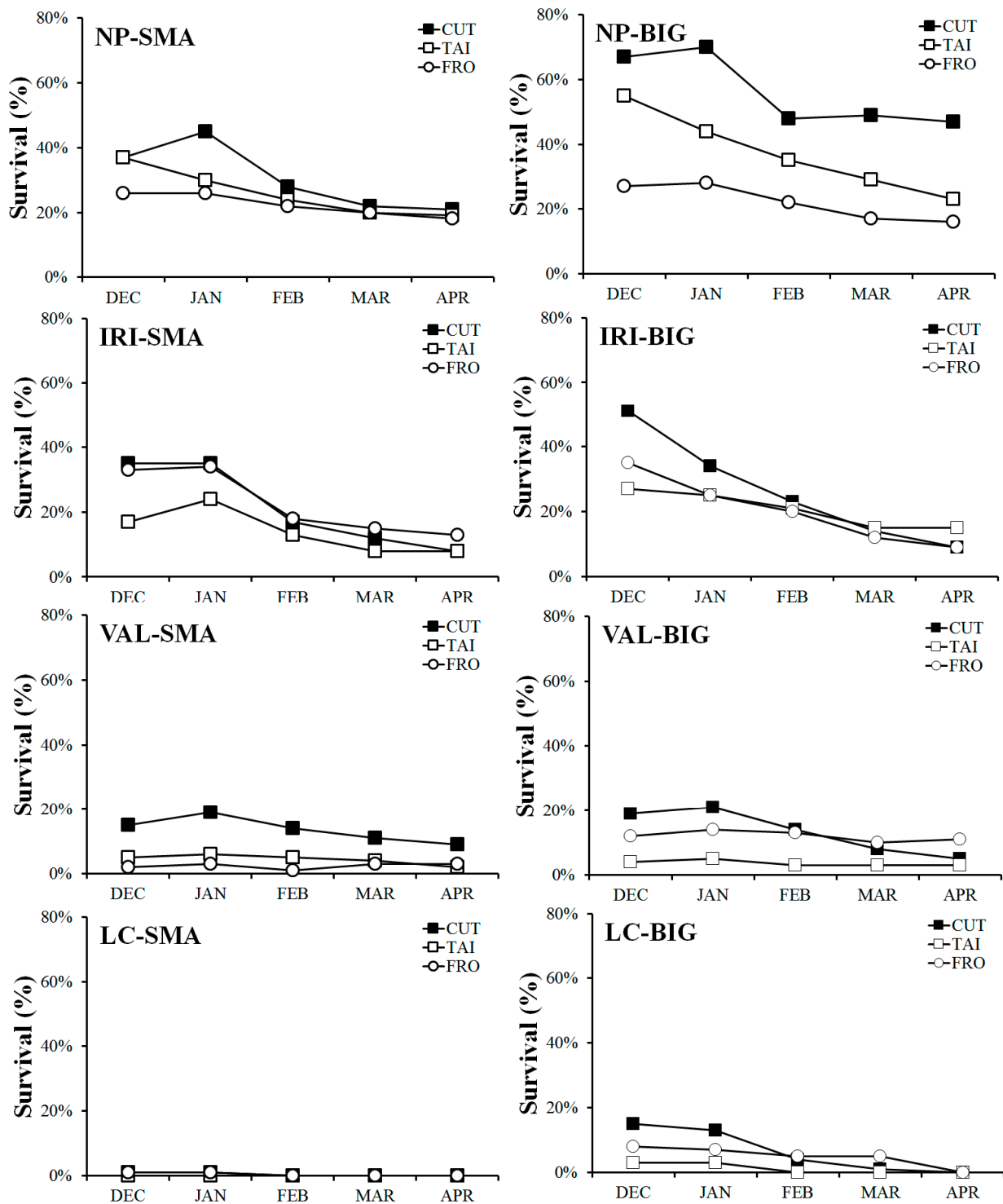

Figure 4. Survival of saplings plantation of *Nothofagus antarctica* among forest treatments (FRO = area just upstream of the old dam, TAI = area where stream enters beaver meadow, CUT = area harvested, but not flooded, by beavers), locations (NP = Tierra del Fuego National Park, VAL = Río Valdez, IRI = Río Irigoyen, LC = Los Cerros), plant type (BIG = big plants, SMA = small plants), and time (month) during the first growing season.

Table 6. Multiple ANOVAs of saplings plantation performance of *Nothofagus antarctica* after one-year among forest treatments (FRO = area just upstream of the old dam, TAI = area where stream enters beaver meadow, CUT = area harvested, but not flooded, by beavers), locations (NP = Tierra del Fuego National Park, VAL = Río Valdez, IRI = Río Irigoyen, LC = Los Cerros), plant type (BIG = big plants, SMA = small plants), an time (month), analysing: SUR = survival (%), H = sapling height (cm), and GRO = growth of the extended dominant branch across the studied growing season (cm month^{-1}).

	Level	SUR	H	GRO
A: Forest	FRO	13.3a	17.5	0.70b
	TAI	13.1a	18.0	0.61ab
	CUT	21.1b	16.3	0.38a
	F	32.40	1.94	4.36
	(*p*)	(<0.001)	(0.144)	(0.014)
B: Location	NP	32.4d	17.8ab	0.53a
	VAL	8.2b	19.2b	0.89b
	IRI	20.3c	17.5ab	0.70ab
	LC	2.3a	14.5a	0.13a
	F	209.89	2.98	5.35
	(*p*)	(<0.001)	(0.032)	(0.001)
C: Type	BIG	18.4b	20.7b	0.56
	SMA	13.2a	13.9a	0.57
	F	32.49	58.94	0.01
	(*p*)	(<0.001)	(<0.001)	(0.921)
D: Time	DEC	22.6c	18.8b	0.12a
	JAN	20.2c	18.3ab	0.14ab
	FEB	14.6b	17.6ab	0.55bc
	MAR	11.6ab	16.4ab	0.72c
	APR	10.0a	15.1a	1.28d
	F	27.88	2.65	17.60
	(*p*)	(<0.001)	(0.033)	(<0.001)
AxBxCxD	F	0.17	1.26	3.16
	(*p*)	(0.999)	(0.240)	(0.001)

F = F test, *p* = probability. Different letters showed significant differences using Tukey test (*p* ≤ 0.05).

4. Discussion

Many studies have examined and characterized the impacts of beavers in both North and South America, including forest structure, microclimate, species assemblage, biodiversity, nutrient cycles and ecosystem functioning [34–37]. However, few studies have investigated the variety of environmental changes associated with beavers from the cut forested areas, the abandoned meadows and the different sub-zones within the meadow itself (e.g., [4,8,38]).

Changes to the water table level is one of the main beaver impacts [4,12], where dams produce an accumulation of sediments and modification in the main soil characteristics (e.g., moisture or nutrient content) [39,40], leading to the establishment of new species assemblages (e.g., grasses) that did not previously dominate in the area [34,36,41]. These changes were also quantified in this study, where the reduction in the overstory and the flooding significantly modified soil moisture (FRO-TAI>CUT-OGF) and soil characteristics. When the beavers were removed or left the area, the natural succession changed in the flooded areas, leading to meadow formation, while in the cut, but not flooded, areas the recovery is following the expected path (e.g., quickly recovering by the dominant forest species) [23,32]. Some authors quantified the impact of the beaver across the Tierra del Fuego archipelago (e.g., [6,14]), and describe some particularities associated to the different ecological areas (e.g., recovery rates and impact degree in steppe areas compared to mountain forests). In our study, we determined that the magnitude of the beaver impact was not homogeneous through the landscape, e.g., changes in the soil characteristics

differed along climate gradients (SM and C increasing with rainfall and decreasing with temperature, and SBD following a contrary pattern). These findings suggest that the trade-offs generated by beavers for the passive recovery can change across the landscape, e.g., nutrient availability can be the main limitation in some areas while the water table can be the limitation in other areas.

Natural regeneration in *N. pumilio* forests quickly reacts to canopy openings [18,23], where seedling banks are the first to respond [42,43] and are complemented with the arrival of seeds during the first years after the impacts [32]. However, beaver dam-induced flooding kills the seedling bank, and few plants are recruited after the abandonment of the ponds. This was previously indicated by other authors [8,38], who suggest the negative interactions with the understory and exotic plants that arrive and compete with forest regeneration [4]. Here, we also define the quantity and quality of seed that arrived at local (areas at each meadow) and landscape level. According to these results, it is possible that the quantity and quality of seeds, as well as litter inputs, limit the normal recovery of regeneration in the meadows. For example, Martínez Pastur et al. [32] suggest that in heavy harvesting areas the main limitation in the regeneration cycle was the quantity of seed and the litter deposition, which is necessary for effective insulation from cold during winter. However, seedling mortality in beaver meadows, having very low canopy cover, was higher than would be expected from natural regeneration dynamics of *N. pumilio* forests [18]. Besides, these changes in the natural regeneration dynamics markedly changed across the landscape, which was identified as a driver of change in other papers related to regeneration and management (e.g., [27,44]).

The trade-offs identified in the literature and our studies point to the lack of recovery in beaver meadows in the short- and medium-term (e.g., up to 20 years) [8], potentially resulting in the loss of more than 30 thousand ha of riparian forests [6,14]. In this framework, passive restoration is not an option according to the magnitude and persistence of the beaver impacts. However, it is not clear which is the best strategy to define restoration alternatives after beaver removal. In this paper, we explore two approaches: (i) maintain the dominant forest species (*N. pumilio*) through plantations and removing the understory competition, where the hypothesis is that the main trade-offs are the lack of regeneration recruitment and the negative influence of grasses (see [4]), and (ii) change the dominant forest species (*N. antarctica*) through plantations without understory removal to decrease the costs, where the hypothesis is that the main trade-offs are lack of physiological adaptations of *N. pumilio* to the new environmental conditions (see [25]). The results showed that active restoration of the first approach is feasible in the medium-term (3 years after plantations reaching survival rates >30–40% in average). However, the variation in beaver meadows greatly affected the performance and effectiveness of the planting and understory removal, e.g., FRO compared to TAI. We tested this approach at one site, being one of the most favourable in the natural regeneration according to forest management studies (e.g., [27,44]) and climate conditions (e.g., [26]). Further studies must be conducted to support these findings at the landscape level.

The second approach allows the restoration of large impacted areas with lower investment (money and human resources) due to: (i) plants can be easily obtained in peatlands, were *N. antarctica* plants grow over the peat and multiply through root sprouts; (ii) bare root plants can be transported directly to the planting sites at the beginning of the autumn or early spring; and (iii) direct plantations in the meadows can be conducted without any previous labour in the field. An additional advantage to this approach is that *N. antarctica* can survive in wetter environments (such as in peatlands) [25], generating a favourable forest environment to promote a second generation of *N. pumilio* forest in the medium-term (30–40 years). Our results show that big plants (15–30 cm height) can achieve promising results for restoring meadows (FRO and TAI) but only in the cooler and wetter climatic conditions (e.g., southern areas close to mountains). These results show that there is not only one restoration strategy that is able to be applied across the variable conditions of the region. Gea et al. [44] stated that the regeneration performance of *N. pumilio* after harvesting

greatly varied across the landscape, being vulnerable to different abiotic and biotic threats. In the same way, restoration efforts face these challenges across the region, making further studies critical to supporting new proposals that increase restoration effectiveness at the landscape level.

5. Conclusions

Beaver impacts were associated with changes in abiotic and biotic environmental stand characteristics, including forest structure, soil properties, understory plants and ecosystem functions. We find that stand characteristics and natural dynamics (abiotic, soil, forest structure, understory, litter, seeding, regeneration) changed within beaver meadows and unimpacted forests across the landscape (Question 1). These modifications influence *N. pumilio* seedling success, including seeding, recruitment and survival. The lack of natural forest regeneration and persistence of herbaceous communities in the impacted areas (meadows) indicate the need of active restoration. Two strategies were explored here, and both are possible to implement according to the climate characteristics of the areas: (i) maintain the dominant forest species with plantations (transplanting bare root plants) and remove the understory competition, and (ii) change the forest species with species that are more adapted to the main soil changes. We find that *N. pumilio* seedlings can survive in the short-term (three growing seasons) in the impacted environments (Question 2), and that early succession forest species (e.g., *N. antarctica*) can improve the active restoration across the landscape (Question 3). However, it is important to highlight that the landscape greatly influenced local conditions, both at local scale (among meadows) and at regional scale (across climate gradients) which can lead to success or failure of the proposed restoration strategy. Further studies are needed to design specific proposals for each climate driver that greatly influences over regeneration performance. Finally, it is necessary to monitor different *Nothofagus* species across natural environments in the landscape to determine the feasibility and effectiveness of different strategies in restoration plans, considering the selection of climate resilient tree species.

Appendix A

Table A1. Summary of variables employed in the study indicating type, name of the metric, acronym, units and brief description of the measurement method.

Type	Metric	Acronym	Units	Measurement Method
Forest structure	Diameter at breast height	DBH	cm	Forest caliper
	Basal area	BA	$m^2\,ha^{-1}$	Criterion RD1000
	Dominant height	DH	m	Trupulse 200 laser rangefinder
	Overstory crown cover	CC	%	Hemispherical photos
	Relative leaf area index	RLAI		Hemispherical photos
	Incidence of total radiation	TR	%	Hemispherical photos
	Distance to the forest edge	DIST	m	Trupulse 200 laser rangefinder
Regeneration	Natural regeneration density	NRD	$n\,m^{-2}$	5×0.2 m plots
	Regeneration browsing	BRO	%	Damages at each plant
Understory cover	Monocots cover	MONO	%	Interception points in transects
	Dicots cover	DICO	%	Interception points in transects
	Non-vascular plants cover	NV	%	Interception points in transects
	Overstory trees	TREE	%	Interception points in transects
	Bare soil	BS	%	Interception points in transects
Soil	Soil bulk density	SBD	$g\,cm^{-3}$	Field borer
	Soil moisture	SM	%	Field borer and dry in stove
	Soil total organic carbon	C	%	Field borer and LECO CR12
	Soil total nitrogen	N	%	Field borer and Kjeldahl
	Ratio carbon/nitrogen	C/N		Using C and N data per plot
	Soil extractable phosphorous	P	ppm	Field borer and Bray and Kurtz
	Cation exchange capacity	CEC	meq 100 gr	Optima 3000 Perkin Elmer
Litterfall	Total seeds	S	$thousand\,ha^{-1}\,yr^{-1}$	Litter-fall traps
	Seed foraged by insects	SI	$thousand\,ha^{-1}\,yr^{-1}$	Damages observed at each seed
	Seed foraged by birds	SB	$thousand\,ha^{-1}\,yr^{-1}$	Damages observed at each seed
	Seed weight	SW	$kg\,ha^{-1}\,yr^{-1}$	Scale at laboratory
	Weight of leaf litter	LW	$kg\,ha^{-1}\,yr^{-1}$	Scale at laboratory
	Small branches of the litter	BW	$kg\,ha^{-1}\,yr^{-1}$	Scale at laboratory
Plantation	Seedling survival	SUR	%	Counting of alive seedlings
	Seedling height	H	cm	Height from bottom to the extended dominant shoot
	Number of leaves	LEA	n	Counting alive leaves per seedling
	Root length	R	cm	Extended root after washing
	Foliar area	FA	cm^2	Using scanner at laboratory
	Leaves weight	LW	gr	Using scale after dry in stove
	Steam weight	SW	gr	Using scale after dry in stove
	Roots weight	RW	gr	Using scale after dry in stove
	Steam/root weight ratio	S/R		Using SW and RW of plants
	Growth	GRO	$cm\,month^{-1}$	Changes in length of the extended dominant branch

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