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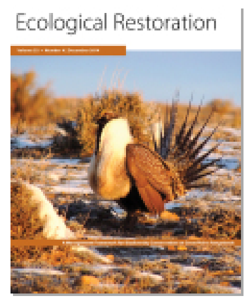

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ABSTRACT

As ecosystem engineers, North American beavers (*Castor canadensis*) change many environmental conditions in watersheds, felling trees, damming streams, and flooding riparian zones. In Tierra del Fuego, where beavers were introduced in 1946, these alterations have produced meadows that appear to be long-term alternate stable states, lacking signs of resilience and natural forest regeneration. The aim of this work was to determine the abiotic and biotic factors that affect native tree seedling success in abandoned beaver meadows in *Nothofagus pumilio* forests. Environmental conditions including light, soil moisture, herbaceous plant community composition, and reinvasion potential were measured in areas impacted by beavers and in unimpacted old-growth forests. Additionally, we monitored the survival and success of *N. pumilio* seedlings transplanted in plots where meadow vegetation was cleared. Tree seedlings showed little growth, and survival varied by type of beaver impact. While survival was high and similar to unimpacted sites in zones cut but not flooded by beavers, it was significantly lower in meadow zones that were previously flooded and cut, compared to old-growth forests. We found that the reinvasion of herbaceous plants into transplantation study plots was negatively related to tree seedling survival, and herbaceous (monocot) plant cover itself was related to beaver-created gradients in soil moisture and light availability. Overall, these abiotic changes modified the meadow's plant community and enhanced herbaceous vegetation cover, particularly monocots and exotics, thus hindering transplanted seedling survival.

Keywords: active restoration, *Castor canadensis*, ecosystem engineer, reforestation, southern Patagonia

At a global scale, invasive species are important drivers of environmental change (Vitousek et al. 1996). By altering disturbance regimes (Mack and D'Antonio 1998), species interactions (Shea and Chesson 2002), and nutrient cycling (Ehrenfeld 2003), many invasive species profoundly modify the biodiversity and function of entire ecosystems. In some cases, these alterations can have medium- or longterm legacies that persist after management of the invasive species and require active intervention to restore natural or desirable conditions (D'Antonio and Myerson 2002). As a result, the practice and study of restoration ecology has become increasingly important to implement programs to remediate and restore crucial ecosystem functions and capacities in the wake of widespread species invasions (Roberts et al. 2009).

The North American beaver (*Castor canadensis*), as an invasive species introduced into Tierra del Fuego in 1946, has extensively altered riparian forests and has become a focus of conservation concern (Malmierca et al. 2011). As ecosystem engineers, beavers generate large impacts on the environmental conditions of streams and riparian zones (Naiman et al. 1988), and their ability to fell trees and build dams creates two distinct types of novel habitats within watersheds. First, the zone where trees are harvested extends approximately 30–60 m from the edge of the beaver pond (Anderson et al. 2009) and results in a reduction of the aboveground tree biomass (Rosell et al. 2005). Similar to the effects of certain silvicultural practices, this moderately augments light radiation and moisture reaching the ground level (Martínez Pastur et al. 2011a). Second, beaver-induced flooding of the riparian zone causes not only the elimination of tree canopy cover in the pond, but also the accumulation of sediment, retention of nutrients, and elevation of the water table, which together lead to increased light radiation, nutrients, and soil moisture

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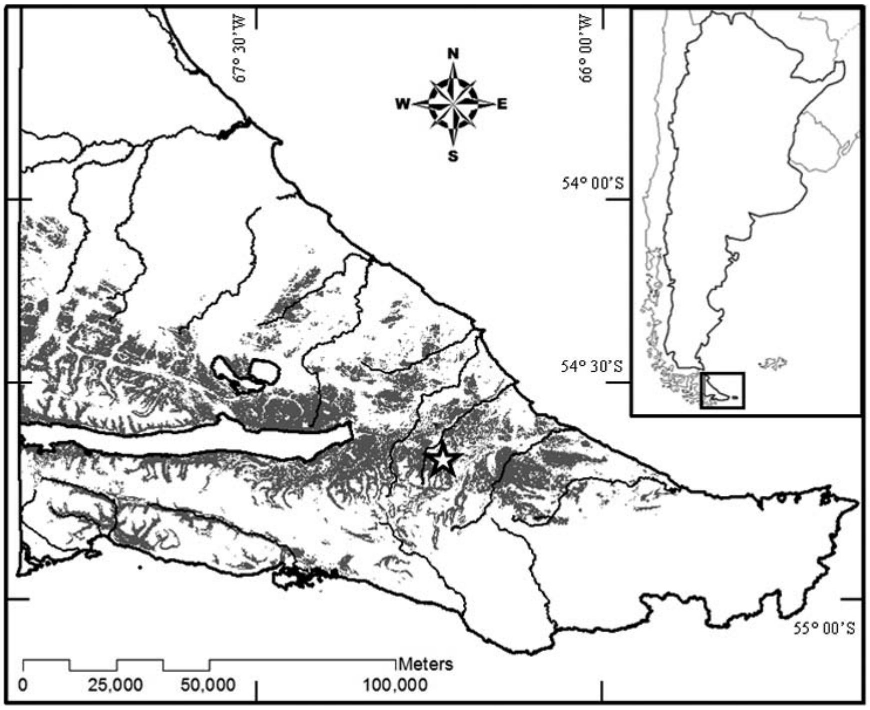

Figure 1. Location of study area in Tierra del Fuego, Argentina. Gray shaded area indicates extension of *Nothofagus pumilio* forest.

availability to plants that recolonize after ponds drain and become meadows (Naiman et al. 1994; McMaster and McMaster 2001; Westbrook et al. 2006). Within the beaver meadow itself, however, there also are gradients of soil characteristics, whereby generally the front of the beaver pond (the area near the dam) is wetter and contains more organic sediment compared to the tail (the area where the stream enters the pond) (Gurnell 1998).

In general, beaver-caused alterations generate greater landscape heterogeneity, providing various habitats for several animal species (Rosell et al. 2005) and increasing plant diversity (Wright et al. 2002). Notably, northern hemisphere riparian tree species commonly harvested by beaver, such as aspen (*Populus* spp.) and willow (*Salix* spp.), have been subject to beaver disturbance for thousands of years and are adapted to the wet environments that beavers engineer by sprouting from roots after herbivory or tolerating wet conditions (Naiman et al. 1988). Alternatively, *Nothofagus* species, the dominant trees in southern Patagonia are not adapted to such disturbances. These tree species are slow-growing, long-lived, and lack a viable seed bank, relying instead on an understory seedling bank to regenerate after natural windthrow or ice damage-caused gaps in the canopy (Cuevas and Arroyo 1999).

While this natural regeneration process of *Nothofagus* is not affected by beaver foraging in the adjacent, unflooded forest, the previously flooded portions lose their seedling bank and show negligible seedling recruitment, even more than 20 years after abandonment (Martínez Pastur et al. 2006). Instead, plant community composition during succession apparently diverges from the natural riparian assemblage as abandoned beaver meadows age, accumulating exotic plant species in the process (Wallem et al. 2010). Considering this evidence, beaver meadows appear to be an alternative or longterm stable state, and therefore active intervention is likely required to achieve forest regeneration over the short and medium term (Anderson et al. 2009, Malmierca et al. 2011).

The aim of this study was to determine the role and relative importance of specific abiotic and biotic factors that influence the survival and success of transplanted *Nothofagus pumilio* seedlings in abandoned beaver meadows in Tierra del Fuego. The following specific objectives were defined in the context of this pilot restoration effort: 1) characterize changes in abiotic and biotic variables in abandoned beaver meadows; 2) measure the growth and survival of *N. pumilio* seedlings transplanted in abandoned beaver meadows; and 3) determine how environmental variables relate to transplanted seedlings' growth and survival. We hypothesized that there are beaver-caused changes in the abiotic and biotic environment of abandoned beaver meadows that are responsible for the observed lack of *N. pumilio* regeneration. Previous experiments have shown that lower or higher light radiation and soil moisture levels can negatively impact *N. pumilio* seedling growth, biomass production, photosynthetic capacity, and other eco-physiological characteristics (Martínez Pastur et al. 2011a). Therefore, understanding how these factors relate to seedling transplantation can help design more effective strategies for active restoration of beaver-impacted ecosystems in southern Patagonia.

Methods

Study Site

The study site was located in the eastern part of Tierra del Fuego Province, Argentina, which is dominated by old-growth *N. pumilio* stands with some *Sphagnum* spp. bogs (54°38′ S, 66°42′ W) (Figure 1). Plots were established in three abandoned beaver meadows along a 1 km stretch of a tributary of the Irigoyen River; beavers have been present in this zone since the 1960s, affecting approximately 2.5% of the surface area, including 30–40% of the stream length (Anderson et al. 2009). Each meadow was approximately 200 m long and 60 m wide with studied zones located approximately 50–150 m meters apart within the same meadow. Mean annual temperature is 4.8°C, averaging 1.5°C during May–September and 7.3°C during October–April, and mean annual precipitation varies between 350 and 456 mm yr^{-1} with an average of 34.3 mm/month (Kreps et al. 2012).

Baseline Environmental Characterization of Sites

For each meadow, four zones were defined: 1) front (FRO, beaver impacted area just upstream of the old dam), 2) tail (TAI, beaver impacted area where stream enters beaver meadow), 3) cut (CUT, beaver impacted area foraged, but not flooded), and 4) control forests (OGF, adjacent unimpacted control forests). Abiotic and biotic characteristics were measured in four replicate study plots per zone (3 meadows × 4 meadow zones × 4 replicate plots = 48 samples).

Forest structure was measured with the Bitterlich (1984) point sampling method (K between 1 and 7), using a Criterion RD1000 and TruPulse 200 laser rangefinder (Laser Technology, USA). In each plot, diameter at breast height (DBH, cm) of all live trees with a DBH > 5 cm, and the height of two dominant trees were measured to calculate tree density (DENS, individuals ha^{-1}), basal area (BA, m^2 ha^{-1}), and total over bark volume (TOBV, m^3 ha^{-1}). Hemispherical photos were taken from 1 m above the ground during January 2013 with an 8 mm fisheye lens (Sigma, Japan) mounted on a 35 mm digital camera (Nikon, Japan) with a tripod and level and were oriented to magnetic north. The program Gap Light Analyzer v2.0 (Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York) was used to calculate relative leaf area index (LAI). For details of inputs and models see Martínez Pastur et al. (2011a).

Volumetric soil water content (VSW, m^3/m^3) was measured in each beaver meadow zone every two hours from November 2012 to May 2013, using DECAGON Em5b data loggers with ECHO EC-5 probes (Decagon, USA). One data logger with five moisture sensors was placed in each beaver meadow zone at one site (4 data loggers × 5 sensors × 6 months).

Understory plant species richness and cover (%) were registered by relevé (50 m^2 plots) methodology (Kent and Coker, 1992) for each site in January 2013. All vascular plants were determined to species level, while non-vascular plants were considered as a different group. Bare ground ([BG], forest soil without vegetation) and debris ([DEBRIS], dead wood more than 3 cm diameter) cover were also estimated. For analysis, plants were grouped in categories: 1) taxa (dicots [DICO], monocots [MONO], ferns [FERN], bryophytes [BRYO]); and 2) origin (exotic cover [EXO]) (Correa 1969–1998; Moore 1983). In addition, cover of these plant groups was visually estimated in 0.5 × 0.5 m plots adjacent to regeneration plots containing transplanted seedlings.

Nothofagus pumilio *Transplantation*

Within beaver impact zones (FRO, TAI, CUT), 36 regeneration plots (3 meadows × 3 zones × 4 replicate plots) were established by clearing all existing vegetation in a 0.25–m^2 area and planting 100 *N. pumilio* seedlings in a 10 × 10 grid. Seedlings were 2–4 years old, were approximately 5 cm tall, and were collected from adjacent forests by carefully removing them from the leaf litter to prevent breaking and losing fine roots. Transplanting occurred in late October 2012, which is before the start of the growing season.

Survival (SURV), apical sprouted bud growth, and number of leaves were measured monthly in each plot from December 2012 to April 2013. SURV was calculated by counting the number of seedlings with green leaves. Baseline survival was taken as the number of live seedlings one month after planting to control for the effect of transplantation (an average of 18 seedlings died in each plot during the first month). Growth and number of leaves were recorded on ten randomly selected plants each month. Growth was measured as the length between the tip of the apical bud and the first bud scale scar left from last year's growth, and number of leaves was counted on the same seedlings.

Soil moisture (SM, m^3 m^{-3}) in the top 5 cm of soil was measured at two random locations using a MP406 moisture probe (ITC, Australia). Additionally, photos of each previously cleared regeneration plot were taken monthly to calculate the re-invasion of understory plants over time (REINV). Percent cover of species other than *N. pumilio* was estimated by using a 10 × 10 grid overlaid on the photos. Plants growing naturally adjacent to the cleared regeneration plots were also measured by visually estimating the percent cover of monocots (MONO) and dicots (DICO) in plots of equal size to the regeneration plots.

Statistical Analyses

One-way ANOVAs were used to analyze differences in environmental characteristics (forest structure and understory plant community composition) with beaver meadow zone as the factor (FRO, TAI, CUT, OGF) and differences between zones were assessed with Tukey HSD post-hoc tests. To avoid pseudoreplication, the measurements from the four replicate plots in each area were averaged before analysis and all forest structure measurements were log-transformed to achieve a normal distribution.

Linear mixed effects models were used to further analyze a selection of the environmental variables along with reinvasion of understory plants and seedling survival. Beaver meadow zone (FRO, TAI, CUT) was input as a fixed effect, while each meadow was input as a random effect. Model fit was

Table 1. One-way ANOVAs of forest structure considering three beaver impact zones studied (FRO = front of the beavers meadows, TAI = tail of the beaver meadows, CUT = areas foraged by beavers) and unaltered control areas (OGF = intact old-growth forests). Values indicate average (± standard error). DBH = diameter at breast height (cm), DENS = tree density (n ha^{-1}), BA = basal area (m^2 ha^{-1}), TOBV = Total over bark volume (m^3 ha^{-1}), CC = canopy cover (%). Different letters within a column indicate significant differences between treatments using Tukey tests ($p \leq 0.05$).

	DBH	DENS	BA	TOBV
FRO	33.2(12.9)	6(0.9)^a	2.2(0.4)^a	27.4(6.3)^a
TAI	39.0(11.8)	12(8.8)^a	3.0(2.2)^a	28.0(18.5)^a
CUT	46.8(4.1)	158(36.7)^b	27.4(3.3)^b	321.2(69.3)^b
OGF	49.3(4.9)	611(113.6)^b	65.3(1.0)^c	852.4(76.8)^c
F(df)	0.5(3)	13.9(3)	16.2(3)	19.9(3)
p	0.51	< 0.01	< 0.01	< 0.01

assessed using a log likelihood ratio test and differences between areas were obtained through F-tests, comparing the intercepts for each zone. The amount of the model variance that was explained by differences between meadows was calculated by dividing the random effect variance by the total variance. All models were run in R (R v2.15.2, R Core Team, Vienna, Austria) using the lmer command from the lme4 package (Bates et al. 2014).

Differences in understory plant communities between meadow zones were assessed using Detrended Correspondence Analysis (DCA). Rare species (species with less than 20% frequency of the most common species) were not weighted.

Variation between sites along with the apparent lack of a direct relationship between seedling survival and many environmental variables observed during initial data exploration led us to develop a conceptual model of the relationships between seedling survival and the environmental variables, which was built based on knowledge of the system and the data presented in this study. Then, the model was tested using a structural equation model (SEM). SEM is designed to test causal networks and confirm direct and indirect relationships between variables (Grace 2006). We built a model based on our predictions; used chi-squared tests to assess model accuracy, then eliminated any path that was not significant ($p < 0.05$). We used standardized path coefficients to describe the relationships between variables. Averages of replicate plots were again used for this analysis to avoid pseudoreplication and to focus on between-site differences. SEM analysis was run in R, using the lavaan package (Rosseel 2012).

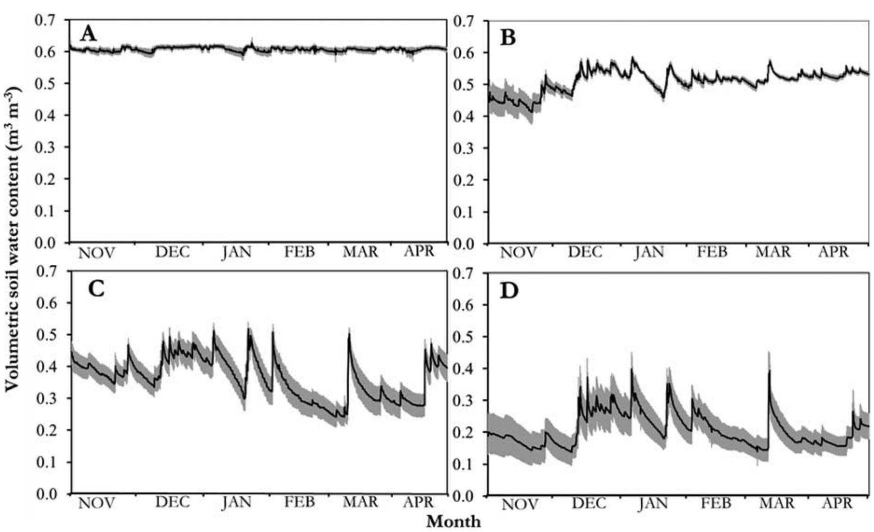

Figure 2. Changes in volumetric soil water content (± standard error, n = 5 samples per measurement) during study period in beaver impact zones and reference sites. A) Front of beaver meadow; B) tail of beaver meadow; C) cut area foraged by beaver; D) intact old growth forest.

Results

Environmental Characteristics

All forest structure characteristics were altered in beaver-impacted zones, except average DBH (Table 1). Sharp decreases in DENS, BA, and TOBV were observed in beaver-affected zones. Meadows (FRO and TAI zones) displayed the lowest values (DENS = 1–2%, BA = 3–5%, TOBV = 3% of OGF value), while decreases observed in CUT zones were less extreme (DENS = 26%, BA = 42%, TOBV = 38% of OGF value).

Soil data loggers revealed a gradient in soil moisture with FRO, TAI, CUT and OGF in order of decreasing values. Additionally, the effects of rain events varied by zone; the FRO and CUT zones showed little variation throughout the season, while CUT and OGF plots displayed marked spikes in soil moisture coinciding with rain events (Figure 2).

The cover of different plant functional groups varied significantly by zone. Less BG was present in meadow impact types (TAI, FRO), compared to CUT and OGF plots. This pattern coincided with significant increases in DICO cover in meadows, while MONO cover increase was marginally significant. Within vascular plant cover, there was also an increase in EXO, while FERN and BRYO cover decreased between OGF and CUT plots and both meadow area types (Table 2).

Table 2. One-way ANOVAs of understory plant cover considering three beaver impact zones studied (FRO = front of the beavers meadows, TAI = tail of the beaver meadows, CUT = areas foraged by beavers) and unaltered control areas (OGF = intact old-growth forests). Values indicate average (± standard error). DICO = dicot cover (%), MONO = monocot cover (%), NAT = native plant cover (%), EXO = exotic plant cover (%), FERN = fern cover (%), BRYO = bryophyte cover (%), BG = bare ground and leaf litter (%), DEBRIS = woody debris (%). Different letters within a column indicate significant differences between treatments using Tukey tests ($p \leq 0.05$).

	DICO	MONO	EXO	FERN	BRYO	BG	DEBRIS
FRO	48.6(9.1)^{b}	17.8(3.9)	20.2(1.0)^{b}	1.0(0.9)^{a}	4.3(0.6)	1.7(1.4)^{a}	26.7(1.4)^{b}
TAI	50.4(4.9)^{b}	14.6(4.7)	18.8(3.6)^{b}	0.0(0.0)^{a}	4.3(0.6)	2.3(1.3)^{a}	28.3(1.4)^{b}
CUT	34.7(4.7)^{ab}	4.6(1.0)	3.6(1.3)^{a}	4.1(0.1)^{ab}	10.0(4.3)	30.0(0.0)^{b}	16.7(1.4)^{a}
OGF	19.6(3.1)^{a}	3.0(0.9)	1.1(0.5)^{a}	10.8(3.2)^{b}	10.0(0.0)	30.0(8.7)^{b}	26.7(2.9)^{b}
F	10.6	4.0	18.4	6.5	1.7	10.0	5.9
p	< 0.01	0.05	< 0.01	0.02	0.25	< 0.01	0.02

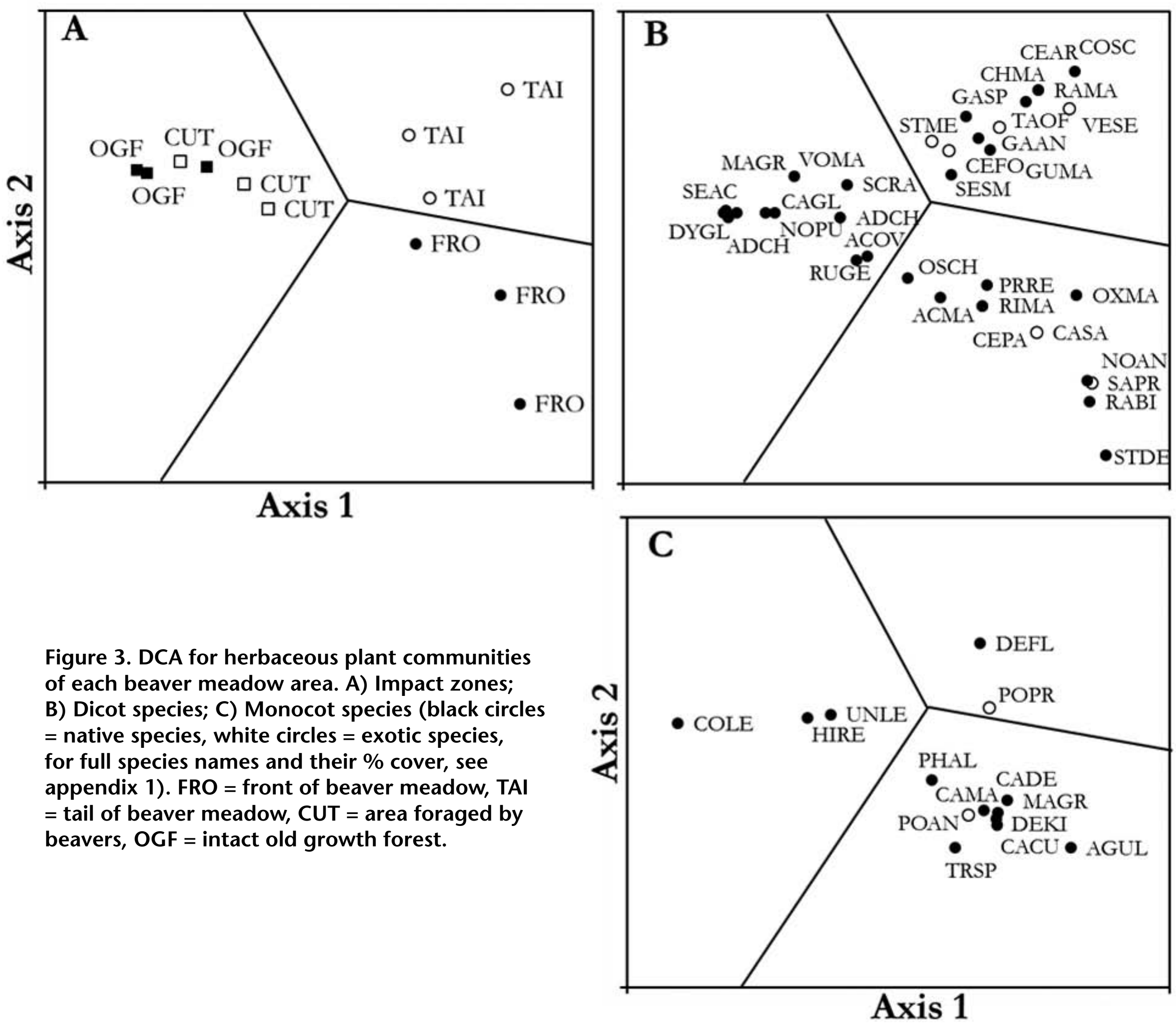

Figure 3. DCA for herbaceous plant communities of each beaver meadow area. A) Impact zones; B) Dicot species; C) Monocot species (black circles = native species, white circles = exotic species, for full species names and their % cover, see appendix 1). FRO = front of beaver meadow, TAI = tail of beaver meadow, CUT = area foraged by beavers, OGF = intact old growth forest.

DCA indicated that while OGF and CUT plant communities were very similar, the FRO and TAI plant communities were different both from each other and from the forest plots (Figure 3A). Dicot species were evenly distributed between zones (Figure 3B), but monocots were more associated with FRO zones (Figure 3C). All exotic species were more associated with meadow zones than CUT and OGF (Table S1).

Table 3. Log-likelihood test results for the effect of beaver impact zones on environmental factors and survival of transplanted seedlings. LL1 = log-likelihood of model with beaver impact zone as fixed effect, LL0 = log-likelihood of null model without impact zones. SITE = percent of model variance that is accounted for by individual meadow sites (random factor).

	LL1	LL0	X^2	df	*p*	SITE
SM	–143.06	–160.04	34.0	2	< 0.01	48.4
LAI	–10.18	19.87	60.1	2	< 0.01	8.4
MONO	–137.88	–158.49	41.2	2	< 0.01	3.4
REINV	–151.61	–158.78	14.3	2	< 0.01	2.3
SURV	–153.60	–157.50	7.8	2	0.02	0.0

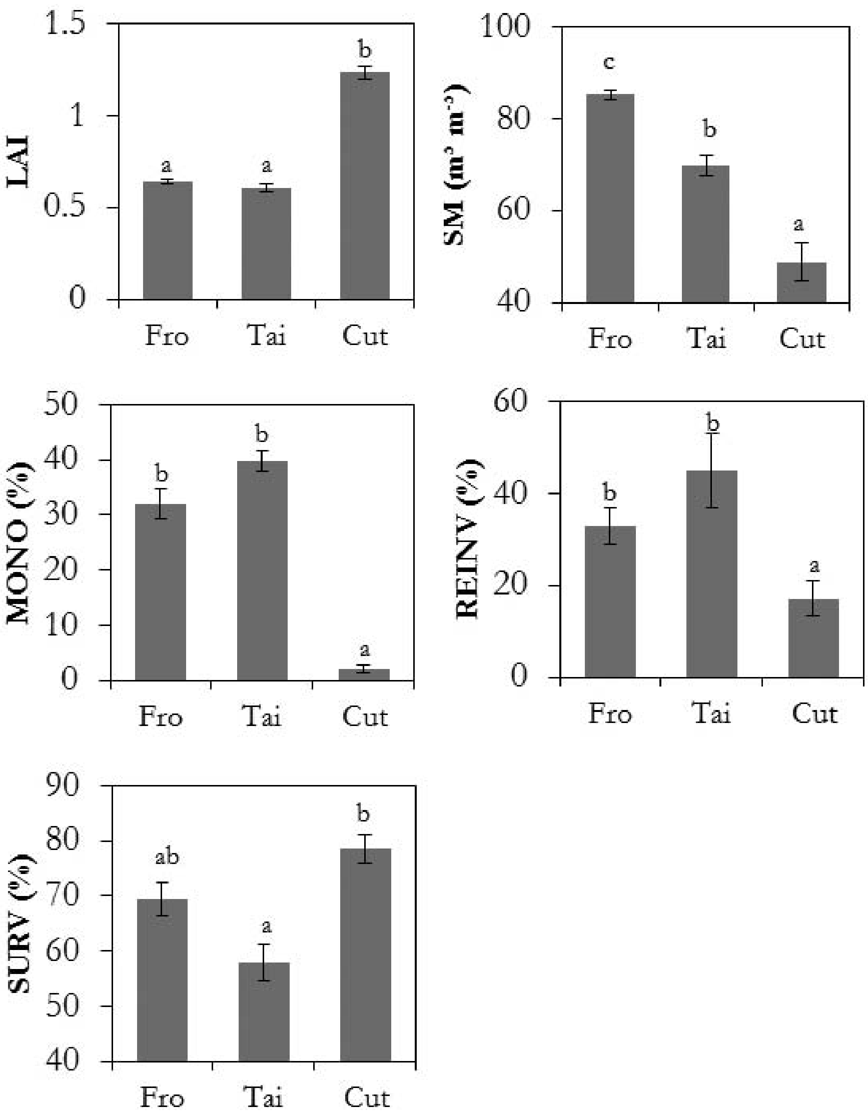

Figure 4. Average values of environmental factors and transplanted seedling survival in three different beaver impact zones (as per Table 1). LAI = Leaf area index, SM = soil moisture, MONO = monocot cover adjacent to regeneration plots, REINV = cover of plants that invaded regeneration plots, SURV = seedling survival. Letters indicate significant differences at the *p* = 0.05 level from F tests from mixed effect models.

Nothofagus pumilio *Transplantation*

Growth and number of leaves were not significantly different between beaver meadow zones. Growth of transplants only occurred during February, when seedlings from all zones grew approximately 3 mm. Seedlings had few leaves with an average of three leaves per plant and no significant change over the growing season.

Beaver meadow zone was a significant factor in seedling survival (Table 3). There was steady mortality in all areas during the season with the highest values found in TAI areas and the lowest occurring in CUT areas (Figure 4). Over the course of the entire study, the seedlings showed very few signs that drought or herbivory were the cause of mortality.

Beaver meadow zone also contributed significantly to differences in SM and LAI (Table 3). LAI was significantly lower in zones within the beaver meadows, compared to CUT zones. Average SM also presented higher levels in beaver meadow zones than the CUT zone, with FRO being the wettest, followed by CUT (Figure 4). However, the random effect of site explained a high proportion of the variance associated with the model, indicating differences between sites in addition to differences between zones within beaver meadows (Table 3).

Beaver meadow zone was also important for REINV and MONO (Table 3). There was a consistent increase in herbaceous plant cover over the growing season, but these increases differed significantly by zone, where there was significantly more reinvasion in the beaver meadows than CUT and OGF. Reinvasion displayed a very similar pattern to MONO, and monocots made up a majority of the reinvading plants.

Environmental Drivers of Restoration

The SEM model revealed that our hypothesized conceptual model (Figure 5) adequately fit our data

(Maximum likelihood ratio test; $X^2 = 11.9$, df = 6, $p = 0.064$), but several hypothesized paths, including those between BA → MONO, SM → REINV, and LAI → REINV, did not add significantly to the model and thus were removed (Figure 5). The resulting model, however, did provide evidence for indirect effects of abiotic factors (moisture and light) on seedling survival mediated through biotic factors (reinvasion of herbaceous plants). The R^2 of each predicted variable was high except for SM, at only 0.4, indicating that there are also other factors that we did not measure affecting the ecohydrology of beaver meadows.

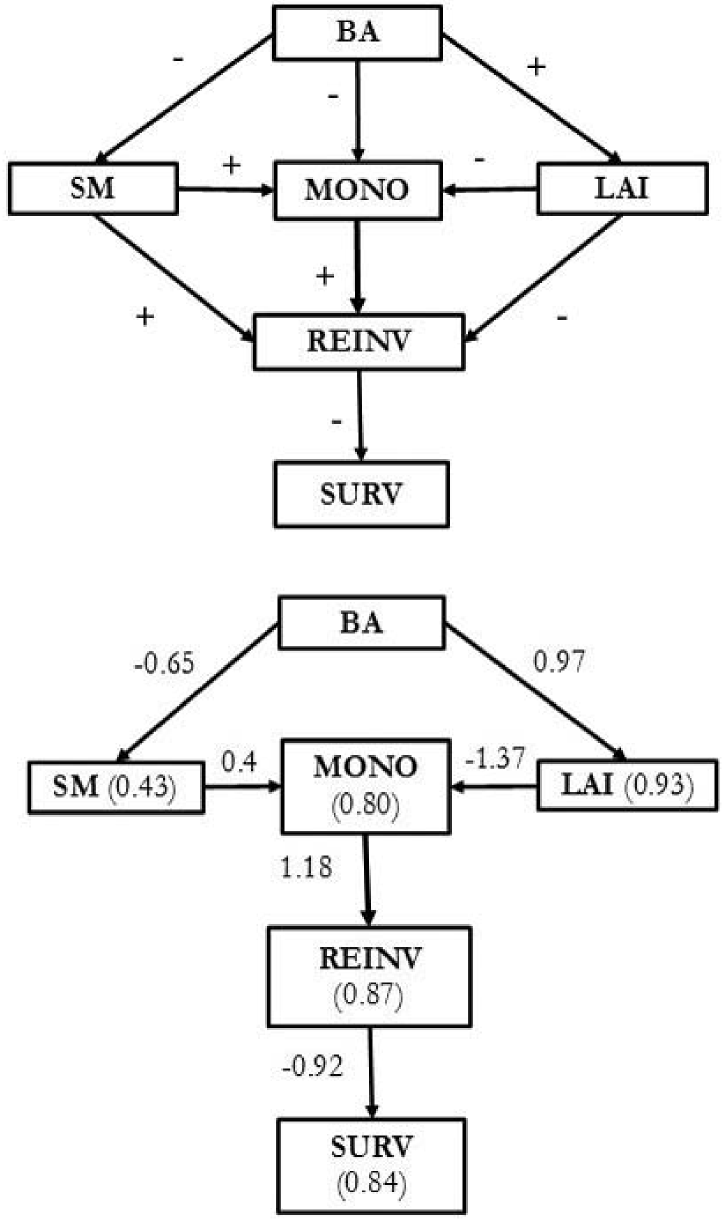

Figure 5. Interactions between environmental factors and transplanted seedling survival in beaver meadows in Tierra del Fuego. First, a conceptual model (A) was developed based on data presented in this study and general knowledge of the study system. Signs on arrows indicate the direction of relationship. Then, the odel was tested (B) with structural equation modelling (SEM) to determine significant causal pathways of transplanted seedling survival. Numbers with arrows indicate standardized path coefficient and numbers in parentheses indicate R^2 for the variable based on this model. Only paths that were significant at the $p \leq 0.05$ level are shown. BA = basal area (m^2 ha^{-1}), SM = soil moisture (m^3 m^{-3}), MONO = monocot cover (%), LAI = leaf area index, REINV = cover of plants that reinvaded regeneration plots (%), SURV = seedling survival (%).

Discussion

Beavers Alterations to Abiotic and Biotic Environmental Characteristics

This study showed that beaver impacts in Tierra del Fuego are associated with interacting modifications to the abiotic and biotic environment that are important in determining the success of *N. pumilio* seedling transplantations in affected riparian zones. While many studies have examined and characterized the effects of beaver in both North and South America, few have investigated gradients of environment changes from the cut forested zone, the abandoned meadow and different zones within the meadow itself, or applied these studies to active forest restoration.

Here, we found that forest structure varied significantly by beaver impact type. While a lack of difference in average DBH between the zones indicated that beaver foraging did not select trees based on size, the strong gradients produced for tree density, basal area, and volume showed the extent to which beavers modify the forest by removing live trees. OGF structure variables largely corresponded to those reported in a previous study of beaver ecology in Tierra del Fuego (Martínez Pastur et al. 2006). Tree density, basal area and volume in impact zones cut by beavers in our study were greater than the average woody biomass removal measured in forests adjacent to beaver ponds in North America (Rosell et al. 2005). The extreme changes in the forest structure of the two beaver meadow impact zones (TAI, FRO) were the result of additional tree mortality due to flooding, subsequently making seedling recruitment more difficult as seeds must arrive from trees remaining in the cut zone or the adjacent undisturbed forest areas (Anderson et al. 2009).

Previous studies have shown that changes in forest structure cause modified abiotic and biotic conditions that are important for *N. pumilio* forest regeneration dynamics, and similar results were found in this study (Martínez Pastur et al. 2013). When compared to OGF, all beaver-impacted zones displayed similar increases in light radiation and decreases in canopy cover (Martínez Pastur et al. 2011a). Soil moisture, on the other hand, had unexpectedly large increases when only considering the effect anticipated from decreased canopy cover. This result indicates a lasting effect on the water table even after dam failure and pond drainage. Additionally, marginally significant differences in soil moisture between FRO and TAI areas correspond to observations by McMaster and McMaster (2001), where areas near dams tended to maintain more moisture. The lack of changes in moisture as a response to rain events in the FRO zones also suggests that the water table is very close to the surface near dams. While alterations to water table levels are probably important in determining this pattern, the accumulation of organic matter, which can generally hold more moisture (Hudson 1994), also could contribute to the soil moisture gradient found in this study.

Increased cover of herbaceous plants, especially monocots and exotic species, in beaver meadows was very similar to previous studies in Tierra del Fuego and is likely due to the increased light and moisture resource levels (Martínez Pastur et al. 2006). This could act as an important barrier to tree seedling recruitment. Hill et al. (1995) described such a case, where increased monocot cover prevented tree establishment in areas where trees were cleared, while Flory and Clay (2010) also found that exotic monocots prevented germination of small-seeded tree species. In this case, the majority of herbaceous plant reinvasion was the result of monocot growth. The ability to spread vegetatively through rhizomes or stolons allowed for the rapid reinvasion of cleared soil (Moore 1983).

The reinvasion measurements that were made in each restoration plot provide information about the vigor of existing vegetation. The relationships observed between abiotic characteristics and the reinvasions of herbaceous plants indicate that resources like moisture and light are important in determining the potential growth of beaver meadow plant assemblages. This result aligns with studies where increased moisture and light levels significantly increased herbaceous biomass, which resulted in increased competition with tree seedlings (Davis et al. 1999). The marginally greater amount of herbaceous plant reinvasion observed in TAI zones is likely due to ideal environmental conditions. While both meadow zones had high light and moisture, the FRO soil was frequently waterlogged during the study, which could have resulted in anoxic conditions that can be harmful for root development (Kozlowski 2002).

Drivers of Transplanted Seedling Survival and Success

Natural *N. pumilio* forest regeneration is characterized by high seedling establishment and mortality in undisturbed forests, where both seedling establishment and mortality decline as canopy cover decreases (Martínez Pastur et al. 2011a). While we did not study seedling establishment, our seedling mortality values in CUT zones correspond closely to patterns observed in the previously cited work's aggregate retention silviculture management treatments. On the other hand, seedling mortality in beaver meadows, having very low canopy cover, was higher than would be expected from natural regeneration dynamics of *Nothofagus* forests (Martínez Pastur et al. 2011a). Additionally, the amount of growth that occurred was very low compared to growth in the greenhouse observed by Martínez Pastur et al. (2011a), which raises concerns about survival over the winter.

Previous greenhouse studies of *N. pumilio* growth and ecophysiology under varying light and moisture conditions indicate that plants grown in high moisture conditions (80–100% soil water capacity) displayed high levels of stress, resulting in lower shoot and root growth and photosynthetic rate, when compared to seedlings grown in moisture conditions of 40–60% soil water capacity. This relationship, however, varied as a function of light availability, where excessive light decreased plant growth (Martínez Pastur et al. 2011b). Light and water stress, which resulted in lower growth in the greenhouse, is likely to be important in the lower than expected survival and growth observed in the wet meadow conditions.

The strong negative relationship between herbaceous plant reinvasion and seedling survival suggests that competition with herbaceous plants is possibly more important than the stress experienced by the seedlings due to excessive moisture and light. This is displayed in the SEM where the relationship between seedling survival and soil moisture and light radiation were indirect, mediated through the amount of herbaceous plant reinvasion that occurred in regeneration plots (Figure 5). Holmgren et al. (1997) would predict that competition within plant communities is more likely in areas of high resource availability. Additionally, Maestre et al. (2009) would put forward that the competitive relationship should also be particularly strong because *N. pumilio* seedlings are adapted to tolerance of low light and moisture conditions, while herbaceous plants present in beaver meadows are more likely to be superior competitors, adapted to take advantage of high resource levels. In fact, controlling competition with herbaceous plants in riparian forest restoration has been acknowledged as important to tree seedling success (Sweeney et al. 2002). While all herbaceous vegetation was removed prior to planting seedlings, continual weeding or the use of chemical or mechanical means to prevent herbaceous plant growth could increase seedling success.

Another general limitation to riparian forest restoration is the effect of herbivore browsing (Keeton 2008). While we observed guanacos (*Lama guanicoe*), a common native herbivore, at the study site during each visit, we found almost no direct evidence of the impacts of guanaco browsing on the planted seedlings. This could be due to the small size of the seedlings, which would cause guanaco browsing to be concentrated on other forage or remove the entire seedling (Cavieres and Fajardo 2005). As seedlings continue to grow and emerge from the herbaceous layer into the understory, the effects of guanaco need to be reconsidered.

Conclusions

Beaver impacts were associated with changes in abiotic and biotic conditions including forest structure, light radiation, soil moisture, and herbaceous plant communities. In turn, these modifications are related to changes in transplanted *N. pumilio* seedling success. Moving forward with efforts to understand how to restore and reforest beaver impacted zones in Tierra del Fuego, further tests of controlling herbaceous species, especially monocots, should be explored as our results suggest that competition is hindering *N. pumilio* success. This could come through modification of the abiotic environment or direct control of monocot cover. As beavers continue spreading north on the mainland and control programs are discussed, understanding what methods of forest restoration are effective is increasingly important.

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Supplementary Table S1 can be found online at: uwpress.wisc.edu/journals/journals/er-supplementary.html.

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